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Spatial patterns of marine biodiversity associated with habitat-forming species on rocky reefs: the Arrábida Marine Protected Area case study

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Abstract

Coastal zones and their rocky reefs are the most productive areas in the world and offer important economic benefits to society and also invaluable ecosystem services. Thus, the study of the biodiversity that supports the basis of food chains and the patterns that determine their spatial variability is of special relevance. The present dissertation investigates the biodiversity composition (taxonomic and functional) and distribution patterns of epifauna associated with four habitat-forming species (HFS) (*Halopteris scoparia*; *Saccorhiza polyschides*; *Sphaerococcus coronopifolius*; *Treptacantha usneoides*). The study was carried out in temperate rocky reefs of four sites at Arrábida Marine Protected Area, mainland Portugal. In this study, Arthropods and Molluscs were the two large taxonomic groups associated with the HFS studied. These groups are characterized by having a free lifestyle, moving freely in the substrate, being mostly detritivores and able to feed on a varied diet. Results showed a spatial segregation of the epifauna in relation to the four HFS studied. Functional structure is less variable among replicates than taxonomic structure, explaining a greater percentage of community variation. *S. polyschides* showed the highest abundance of epifauna, probably due to the greater amount of available habitat compared to the other HFS. *T. usneoides* showed the lowest abundance despite its size and biomass, possibly not being favored by the hydrodynamic conditions found at the time of sampling (stronger sea currents). Despite its small size, *H. scoparia* was important for a large number of organisms that, possibly, found in this HFS a favorable texture to find shelter and refuge. The DistLM showed that density of surrounding algae, mean depth and number of refuges, were also important variables to the biodiversity patterns observed. These results can contribute to a more effective management of marine protected areas, if integrated as an important piece of knowledge for a more complete understanding of ecological networks.

Key-words: Temperate rocky reefs; macroalgae; habitat-forming species; functional traits; biodiversity

Resumo alargado

A costa portuguesa apresenta grande diversidade morfológica e é caracterizada por uma mistura de praias rochosas e arenosas, expostas, semi-expostas e abrigadas. Estes ecossistemas costeiros são reconhecidos como locais de elevada produtividade, fornecendo bens e serviços de valor muitas vezes inestimável. A perda de habitats e biodiversidade marinha é um desafio constante um pouco por todo o mundo. As políticas ambientais internacionais e da União Europeia definem estratégias para reverter e mitigar a pressão humana sobre o Oceano, sendo uma das estratégias mais comuns em curso a criação de áreas marinhas protegidas (AMPs). O Parque Marinho Professor Luiz Saldanha foi a primeira AMP em Portugal continental com um plano de gestão, totalmente implementado desde 2009. Este Parque Marinho localizado na Arrábida é adjacente a um parque terrestre (criado em 1978), e só em 1998 a porção marinha foi designada como área protegida. A AMP abrange cerca de 5300 hectares, com profundidades variadas até 100 metros. Encontra-se dividida em oito zonas com regulamentos variados, desde zonas totalmente protegidas, onde não são permitidas atividades, até zonas parcialmente protegidas, onde grandes embarcações de pesca comercial são proibidas, mas a pesca artesanal sustentável é permitida e regulada. Esta AMP foi criada para proteger habitats e espécies únicos, podendo-se encontrar desde recifes rochosos a florestas de macroalgas, sendo dois habitats de elevada importância para espécies que encontram neles abrigo, locais ideais para reprodução ou alimentação. Quanto maior for o conhecimento sobre estas comunidades biológicas e os seus padrões naturais, melhor e mais adequada será a resposta dada para a proteção das comunidades e ecossistemas que delas dependem.

O estudo realizado no âmbito desta dissertação teve como principal objetivo avaliar a biodiversidade da epifauna marinha associada a quatro espécies de macroalgas, aqui analisadas como importantes espécies-formadoras de habitat (HFS). Esta avaliação foi realizada tanto a nível taxonómico como funcional, onde, para além do estudo dos padrões de distribuição espacial dos macroinvertebrados, também as variáveis que podem influenciá-los foram analisadas. Variáveis essas relacionadas com a morfologia da própria macroalga, e com o ambiente envolvente, todas elas relacionadas com a complexidade do habitat. Três replicados de cada uma das quatro espécies de macroalgas (*Halopteris scoparia; Saccorhiza polyschides*, *Sphaerococcus coronopifolius e Treptacantha usneoides*) foram recolhidos durante o mês de novembro de 2020, com recurso a mergulho com escafandro autónomo, em quatro locais de estudo: dois na área de proteção total (T1 e T2) e dois na área de proteção complementar (C1 e C2). Estas espécies foram selecionadas devido à sua relevância na área de estudo. Foram também recolhidas variáveis relacionadas com a complexidade estrutural do habitat rochoso envolvente, tais como: densidade de algas, complexidade estrutural e número de refúgios presentes. As macroalgas foram recolhidas com recurso a um saco de rede (500µm), sendo estas envolvidas pelo mesmo desde o topo até á base, num movimento rápido efetuado por dois mergulhadores experientes (prevenindo a fuga de organismos móveis associados). Após a recolha, as HFS foram colocadas em caixas térmicas, com água e oxigenação, até chegarem a laboratório, onde foram lavadas e triadas com recurso a crivo de ø200/203mm de malha para se recolher todos os organismos a elas associados. Após triagem, os organismos foram conservados em frascos com álcool a 70%. Todas as macroalgas recolhidas, foram ainda fotografadas, pesadas e posteriormente secas em mufla, para posterior análise fractal e quantificação da biomassa. A epifauna foi, numa segunda fase, analisada com recurso a microscópio monocular e identificada, com ajuda de guias de identificação, até ao nível taxonómico mais baixo possível. Todos estes procedimentos foram realizados no Centro de Ciências do Mar e do Ambiente, da Faculdade de Ciências da Universidade de Lisboa (ARNET-MARE-ULisboa). Os resultados obtidos foram analisados com recurso a análises multivariadas, nomeadamente PERMANOVA e análise de coordenadas principais (PCO). Um modelo linear baseado em distância (DistLM) foi também utilizado.

Adicionalmente, uma análise SIMPER foi realizada para identificar os taxa e traits que mais contribuem para as diferenças entre HFS.

A análise estatística dos dados obtidos mostrou a existência de uma separação espacial da epifauna pelas HFS. Os grupos taxonómicos correspondentes a Chordata, Echinodermata, Nemertea e Platyhelminthes representaram menos de 0,5% da abundância total das amostras, não possuindo valores representativos. O grupo dos artrópodes e moluscos foram os mais abundantes em todas as espécies de HFS, encontrando-se a presença de organismos com hábitos alimentares maioritariamente detritívoros ou omnívoros, possuindo um estilo de vida livre. A menor abundância de macroinvertebrados foi registada em *T. usneoides* e a maior em *S. polyschides*. *S. polyschides* é uma HFS que se destaca pela elevada quantidade de habitat que oferece (maiores valores de biomassa, altura e largura registados entre HFS), possuindo provavelmente uma maior disponibilidade para a presença de mais organismos, com tamanhos potenciais também maiores (quando em comparação com as restantes HFS). A epifauna é composta maioritariamente por moluscos que se encontram em associação com os bolbos desta. Seria de esperar que *T. usneoides* apresenta-se valores de abundância elevados, o mesmo não se verifica apesar do seu tamanho e biomassa, parecendo sair desfavorecida nas condições vigentes aquando da campanha de amostragem (correntes marinhas mais fortes). Possui, maioritariamente, organismos com capacidade ativa para andar, nadar ou “agarrar-se” a esta HFS, sendo capazes de ultrapassar condições mais fortes de hidrodinamismo. *S. coronopifolius* possui níveis intermédios de abundância de macroinvertebrados. A sua comunidade é constituída principalmente por artrópodes que vivem livremente nesta HFS, dependendo apenas da deposição de detritos para alimentação. Sendo uma HFS muito ramificada e com textura membranosa, as suas frondes retém os detritos necessários ao sucesso alimentar da epifauna associada. Esta HFS, possui elevado potencial para se tornar uma macroalga importante para o estudo mais completo das suas redes ecológicas. Num estudo de Franco (2007) realizado na mesma área geográfica, verificou-se que esta macroalga possui uma presença constante no recife ao longo de todos os meses do ano. Apresentando os maiores valores de abundância relativa, registou o maior número de peixes juvenis associados, tendo sido utilizada por todas as espécies de peixes capturadas, parecendo assim ser essencial para o seu assentamento e recrutamento. Sendo assim, também, inevitávelmente importante para níveis tróficos inferiores, como os macroinvertebrados estudados, que são o alimento dominante de peixes nos estágios iniciais de vida. *H. scoparia* parece “ocupar” um lugar de destaque entre as HFS, pois, apesar de possuir tamanhos reduzidos, esta HFS revelou-se importante para a comunidade de epifauna. Possivelmente devido a sua textura e espeto arbustivo, propicia um substrato favorável para refúgio e abrigo, sendo as suas frondes reduzidas em tamanho favorecidas em contraste com frondes de maiores dimensões (como é o caso de *T. usneoides*). A epifauna encontrada nesta HFS possui tamanhos potenciais reduzidos, sendo maioritariamente crustáceos, como são exemplos as famílias Aoridae e Stenothoidae, que se destacam pela sua elevada abundância nesta HFS. Importante referir também, a existência de algumas associações exclusivas entre a epifauna e determinadas HFS. A presença de aranhas-do-mar da classe Pycnogonida, um grupo de predadores com características gregárias e carnívoras, em *H. scoparia* parece sair favorecida, devido á textura filamentosa desta HFS. *Stenothoe spp* aparece exclusivamente em associação a *S. coronopifolius*, provavelmente possuindo uma baixa sensibilidade aos metabólitos secundários produzidos por esta HFS, metabólitos estes que atuam como aleloquímicos dissuasores, impedindo muitas vezes a permanência de macroinvertebrados nas suas frondes. Para além das variáveis morfológicas relacionadas com as HFS, a análise de dados multivariados incluiu também nos modelos obtidos variáveis relacionadas com o ambiente envolvente. Foi incluída a densidade de macroalgas envolventes (correspondentes a *T. usneoides* e *S. polyschides*) e número de refúgios com 5-15cm. Estas variáveis revelaram-se importantes medidas de aumento da complexidade de habitat, fornecendo maior heterogeneidade, maior área e maior diversidade de nichos disponíveis para refúgio e habitação. Profundidade média foi outra das variável adicionada nos modelos.

Sabemos que quanto maior a profundidade estudada, menor o movimento das águas, e mais reduzidos são os níveis de luz, sendo as HFS normalmente de menor tamanho, no entanto isto não significa que a epifauna associada a estas seja também reduzida. Em determinados casos, tanto a epifauna como várias espécies de peixes procuram estas zonas mais profundas e abrigadas, levando à presença de uma elevada abundância de espécimes, o que poderá ter ocorrido também no nosso caso de estudo, sendo que futuros estudos são necessários para se confirmar esta relação positiva.

Seria importante em estudos futuros aprofundar os conhecimentos aqui obtidos. Sendo relevante incluir uma análise temporal, visto que as macroalgas mudam a sua composição nos recifes consoante a época amostrada, o que poderá influenciar a estrutura da comunidade de macroinvertebrados. A manipulação da morfologia algal, bem como a inclusão de novas medidas morfológicas, seriam também importantes medidas a adotar em estudos futuros. Este estudo releva-se um esforço importante no estudo das comunidades de epifauna, que são muitas vezes desvalorizadas, devido à dificuldade na sua análise e identificação em laboratório. Obtiveram-se dados essenciais sobre a composição e importância ecológica dos espécimes que estão na base de redes ecológicas suportadas por recifes rochosos temperados, podendo, para além do acréscimo no conhecimento, contribuir para uma gestão mais eficaz das AMPs.

Palavras-chave: Recifes rochosos temperados; macroalgas; espécies-formadoras de habitat; características funcionais; biodiversidade

Contents

List of Figures

List of Tables

General introduction

The Ocean is the foundation of all life, an extraordinary and unexplored place, teeming with fascinatingly diverse plants and animals which, together with its inhabitants and environmental conditions, shape our planet (Costanza, 1999; Costanza et al., 2014). According to Liquete et al. (2013), oceans, and particularly coastal areas, contribute more than 60% to the total economic value of the biosphere. Thus, marine environments also support a wide variety of services for humans, from recreational activities to obtaining food (Holmlund & Hammer, 1999). The Ocean drives our weather and climate, plays a key part of the water cycle, provides protein to three billion humans and every plant, vegetable and animal has grown through access to water produced through the water cycle driven by the Ocean (Costanza, 1999; Sala & Knowlton, 2006). Although marine species richness may only total 4% of global diversity, life began in the sea, and much diversity is still primarily or exclusively marine (Singh & Ort, 2020). Organisms are distributed in different areas of the oceans; about 98% of the organisms are benthic and only 2% of the organisms are pelagic (Costello & Chaudhary, 2017). Most benthic organisms inhabit the intertidal fringe or shallow sublittoral zones and only 1% live below 2000m (Krogh, 1934). Although these percentages are strongly influenced by the knowledge of the different areas, within each area of the ocean there are different forms of habitat and each organism adapts, in a certain way, to the place where it lives. Habitat is understood to be the specific place in the environment where organisms live, being affected by both abiotic (light intensity, food availability, hydrodynamic characteristics, temperature, salinity, habitat structure, etc.) and biotic (predation, competition, recruitment, symbiosis, etc.) factors (Ashcroft et al., 2011; Constable et al., 2016; Milner et al., 2015; Puente et al., 2017). Marine ecosystems support a high complexity of interactions, these interactions are vital to ecological processes underpinning the proper functioning of ecosystems. In fact, the relevance of distinct species in the functioning of ecosystems is not only related to the complexity of their interactions (e.g. species with multiple interactions in ecological networks), but also to the uniqueness of these species in the balance of ecological networks (e.g. species with unique functions in ecosystems), namely habitat-forming species (HFS) (Angelini et al., 2011; Ellison, 2019; Lemieux & Cusson, 2014).

Habitat-forming species (HFS) are spatially dominant organisms whose biogenic structure enhances species coexistence through the creation of fine-scale, complex matrices in which smaller organisms find refuge from competitors or predators (O'Leary et al., 2017; van der Zee et al., 2016). HFS´ can also modify the metabolic rates of associated species and modulate energy and nutrient flow~~s~~ through the system (Baiser et al., 2013). Macroalgal forests are dominant habitat-forming species in rocky intertidal and subtidal habitats around all European coasts. They contribute to the development of coastlines providing cleaner water through the filtration of nutrients and protecting shorelines from erosion by attenuating and dissipating wave energy (Stachowicz, 2001). Moreover, they enhance coastal primary productivity and are recognized hotspots of diversity, providing abundant food source for a diverse and abundant fauna of mobile benthic invertebrates (Teagle et al., 2017; Wernberg et al., 2009), normally dominated by amphipods, isopods, gastropods and polychaetes (Pereira et al., 2006; Win, 2011). Constitute both reproduction and nursery sites for many other large species, where juveniles find effective shelter from predators and adequate foraging grounds (Stuart-Smith et al., 2015; Thomsen et al., 2016; Win, 2011). It is then expected that many organisms will depend on HFS for their survival. They have the ability to produce large biogenic structures with numerous biota associations, but at different scales and complexities (Mangialajo et al., 2008; Steneck et al., 2002). These structures that form complex and productive three-dimensional habitats (Fulton et al., 2019) are characterized by the enormous biodiversity they support (Teagle et al., 2017), leading to the creation of conditions for a constant improvement of the biological habitat (Mangialajo et al., 2008; Moore et al., 2007; Steneck et al., 2002). For these reasons, macroalgae are also considered important *ecosystem engineers* (Crotty et al., 2019) and key species (Falkenberg et al., 2021), playing a fundamental role in the maintenance and survival of a large part of the coastal marine macrofauna. Recent climate change has, either directly or indirectly, driven widespread losses of marine HFS, which in turn has invoked biodiversity declines and community reorganization. Climate-driven substitutions of HFS can also result in depleted levels of biodiversity and significant structural changes in associated communities (Falkenberg et al., 2021; van der Zee et al., 2016). Human impacts on HSF have accelerated over the past four to five decades (Chen et al., 2021), and in this context, Marine Protected Areas (MPAs) are essential to combat and try to reverse the effects of pressure on habitats.

The International Union for Conservation of Nature (IUCN) defines a marine protected area (MPA) as "any area of intertidal or subtidal terrain, together with its overlying water and associated flora, fauna and historical and cultural features, which has been reserved by law or other effective means to protect part or all of the enclosed environment" (Kelleher, 1999). MPAs are one of the most practical approaches to ocean conservation, being an area of sea that restricts human activity for conservation purposes, primarily dedicated to protecting and maintaining biodiversity, but also to help managing marine resources in a sustainable way, with a holistic, ecosystem-based approach (Cardoso-Andrade et al., 2022; Grorud-Colvert et al., 2021; Marcos et al., 2021). Today, nearly 8.16 % of the ocean is covered by MPAs; of which near 2.4 % is fully or highly protected from fishing (UNEP-WCMC & IUCN, 2022). Scientific studies show that MPAs (totally or partially protected), when working properly, increase the biomass, abundance, and average size of exploited marine species, inside and outside their limits (Grorud-Colvert et al., 2021; Agardy, 1994), providing social and economic benefits (Niccolini et al., 2019; Sala et al., 2013). MPAs can also offer a nature-based solution to help ecosystems and people adapt to the effects of climate change in the oceans (McLeod et al., 2009; Roberts et al., 2017).

The structure of a biological community is shaped by several interacting factors, leading to a highly complex system where the relative influence of each factor is difficult or impossible to isolate (Chemello & Milazzo, 2002; Taniguchi et al., 2003). One of the important challenges of today's ecology is to understand and predict the link between biodiversity and ecosystem functions. Biodiversity, defined as the diversity of life on Earth at all its scales, from genes to ecosystems, as well as all of its ecological and evolutionary processes that sustain it (Sala & Knowlton, 2006), is essential for survival, maintenance, and evolution of ecosystems. Different studies have indicated that communities that are richer in species use resources more efficiently (Hooper et al., 2005). This makes the study of biodiversity really important, not only for contributing to the description of new species, but also for the knowledge of their distribution and, also, for playing a vital role in the maintenance of ecosystem functions, since biodiversity influences the biogeochemical processes and stability (Gamfeldt & Bracken, 2009). In addition, different studies have also shown that the most diverse habitats are more resistant to environmental and anthropogenic changes (Benedetti-Cecchi, 2009). Understanding the patterns and origin of spatiotemporal variation of natural communities thus becomes one of the main goals of modern ecology (Jackson & Blois, 2015; Rapacciuolo & Blois, 2019; Ricklefs, 2004; Witman et al., 2004).

The present dissertation focuses on two main aims: (1) to examine the relative role of marine macroalgae, as HFS, in the taxonomic and functional structure of epifauna, and (2) assess whether macroalgal and surrounding environmental differences influence the distribution of the algae HFS and associated macrofauna in the rocky reef of Arrábida MPA. This study is presented in a scientific article that will be submitted to an international journal quoted in the "Science Citation Index."

1. Introduction

Although the most accessible marine environments, such as estuaries, intertidal areas, and shallow sublittoral areas, are well studied, it is estimated that only 10% of marine species have been described (Appeltans et al., 2012; Singh & Ort, 2020). Rocky reef ecosystems are areas of rock and boulders usually close to coastal regions, dominated by formations of rocks from different origins (limestone, basalt, and granite). These areas are one of the most highly productive in the ocean (Msangameno, 2016; Satyam & Thiruchitrambalam, 2018), as a result, they are important to commercial and recreational fisheries around the world, providing the population with ecosystem services worth billions of dollars annually (Beaumont et al., 2008). Yet rocky reefs occupy only a small portion of the world's total marine area (Henseler et al., 2019). The main habitat-forming species (HFS) of temperate rocky zones are macroalgae belonging to Laminariales and Fucales orders (Bertocci et al., 2014; Mangialajo et al., 2008; Steneck et al., 2002), sharing a dynamic of competition for the domain of rocky bottoms. Fucales dominate a large part of the Mediterranean, presenting several endemic species (Thibaut et al., 2005), while Laminariales dominate much of the remaining temperate zones (Filbee-Dexter & Wernberg, 2018). The regression, and even disappearance, of macroalgae forest is occurring at large scale related to a variety of different stressors, such as pollution, coastal development and urbanization, outbreaks of grazer populations, species introductions and climate change. Besides global stressors, multiple local stressors, such as abandoned fishing gear (nets, trammel nets, threads) and trampling, threaten local and restricted macroalgae populations. The decline or disappearance of Treptacantha forests from many Mediterranean areas is leading to severe habitat transformations, with the loss of three-dimensional structures and associated biodiversity (Thibaut et al., 2005). The available literature suggests that the recovery of fucoid populations can take decades, due to their poor dispersal ability and the slow population dynamics.

In this context, marine protected areas (MPAs) appear as the main tools used by scientists today to achieve the sustainability of the oceans. Arrábida MPA presents natural features that provide good conditions for the presence of a high biodiversity, unique in Portugal and Europe (Batista et al., 2015; Martínez-Ramírez et al., 2021). Its rocky reefs are rich in canopy-forming algae, that constitute a semi-closed biodiversity loop, containing a self-sustained food-web, which include the main algal host and their epiphytic algal assemblages as a basal trophic level, direct mesoherbivore grazers and detritivores as intermediate levels and small fish and invertebrates' predators as high within-canopy trophic levels. Persistence and resilience of these systems are dependent on the diversity of the most important functional groups, such as herbivores (Cacabelos et al., 2010; Steneck et al., 2002). Classic methods of measuring biodiversity, such as species richness and diversity indices, assume that all species are equal; all individuals are the same regardless of their size; and species abundances are correctly assessed with the right tools (Moreno et al., 2017). Species are not all the same, do not have the same ecological characteristics, or have the same effect on ecosystem functioning (Kovalenko et al., 2012). Functional categorization of marine species has proven to be a valuable tool for detecting environmental change, linking shifts in structure to ecological function (Micheli & Halpern, 2005). Measuring functional diversity is measuring the diversity of functional traits, where these are components of an organism's phenotype that influence the ecosystem (McCary & Schmitz, 2021). Functional diversity is calculated by defining functional groups based on morphological and/or behavioral characteristics (e.g., diet, feeding methods, preferred habitat, etc.). The ecological relevance of functional traits in ecosystem processes has led to an increasing number of studies focused on this subject in the marine environment (Bustamante et al., 2014; Guillemot et al., 2011; Henseler et al., 2019).

Due to the key role of epifauna in the conservation of systems dominated by important HFS as macroalgae, we should improve our understanding of the factors that drive species distribution (Bremner et al., 2006; Guillemot et al., 2011; Rufino et al., 2017). Long-term observations of these factors are often scarce, which compromises the ability to report changes in ecosystems (and identify processes that gave rise to such changes) (Ashcroft et al., 2011; Kunze et al., 2021; Puente et al., 2017). Different algal architectures influence the patterns of types and ecologies of taxa in a region, as well as abundance and size of its structure (Lacerda, 2014; Mauffrey et al., 2020). Macroalgal systems of high morphological complexity support greater faunal abundance and diversity than less complex systems (Chemello & Milazzo, 2002; Pereira et al., 2006). Although the mechanisms responsible for this positive relationship are not fully understood, many authors have suggested that greater morphological complexity increases epifauna diversity and abundance by reducing predation, competition, and physical disturbance, while increasing the number of niches and food availability (Cacabelos et al., 2010; Leite et al., 2009; Veiga et al., 2014a). There is a positive relationship between the size of macrophytes and the abundance and diversity of their associated epifauna, since the greater the size, the greater the colonizable area available for the fauna (Machado et al., 2015; Tuya et al., 2011a). Different studies have shown a greater abundance and diversity of epifauna associated with macroalgae, with an increase in algal volume, biomass, or area. However, greater amount of habitat does not necessarily indicate greater complexity (Gee & Warwick, 1994; Hooper & Davenport, 2006; Torres et al., 2015). Fractal geometry has proved to be especially useful for estimating the structural complexity (i.e., estimate the actual structural arrangement that the organism occupies and the spaces available for the epifauna), being used to explain forms found in nature that cannot be framed in the molds of conventional mathematics (Gee & Warwick, 1994).

In addition to this HFS architecture perspective, physical factors (abiotic) such as temperature, salinity, nutrient availability, wave action, depth, and temperature and biological (biotic) factors, such as competition for space and predation, also play an important role in the distribution of communities (Cebrián & Ballesteros, 2004; Freter & Manly, 1977; McAbendroth et al., 2005; Russo et al., 1991; Silva et al., 2021). Temperature is undoubtedly one of the main factors at biogeographic scale, controlling macroalgae distribution, being a factor that takes relevance due to the current state of climate change, mainly driven by ocean warming (De Azevedo, 2019; Fernández, 2011; Filbee-Dexter & Wernberg, 2018; Teagle & Smale, 2018; Wiencke et al., 2014). At micro-scale other environmental factors stand out in the distribution of communities in rocky reef areas (Navarro-Barranco et al., 2021; Sánchez-Moyano et al., 2000a; Snelder et al., 2019; Vázquez-Luis et al., 2009), elucidating relationships between measures of physical habitat and ecological health. Geomorphology can explain changes at regional or local scales (Ruitton et al., 2000; Tuya et al., 2011b), highlighting the structural complexity, which can be measured through the combined topography index (CTI) (Henriques et al., 2013; Pais et al., 2013, 2014). Rugosity is likewise a key geomorphological variable for biodiversity as it creates a range of micro-habitats that promotes species coexistence (Alexander et al., 2009; Mazzuco et al., 2020), being based on diversity of elements and their spatial arrangement (Sala et al., 2012).

This study develop a comprehensive assessment of the taxonomic and functional structure of the benthic macrofauna communities associated with four HFS, and its ecological role in the rocky reefs of the Arrábida MPA. In addition, it also contributes to the assessment of the role of algal morphology and surrounding environmental variation in the structure of communities and inevitably in the structure of trophic webs in these rocky reef zones. Temperate rocky reefs are, worldwide, zones of high biological importance, with high productivity and essential resources to preserve and thus, improving knowledge for a better understanding of the variables that control the existing patterns of biodiversity are essential and can also contribute to a more effective MPA management.

2. Material and methods

All data were collected under the ReefNets project (PTDC/BIA- ECO/28687/2017): "Using ecological networks to predict marine ecosystem responses to human threat”.

2.1 Study area

Arrábida MPA, officially named as Professor Luiz Saldanha Marine Park (PMLS), located on the west coast, is the first Marine Protected Area (MPA) established in mainland Portugal (Figure 2.1 and 2.2). It was named in honor to the famous Portuguese marine biologist Luiz Saldanha (1937-1997), who dedicated his career to studying this region. This MPA was created in 1998 as an extension of Arrábida Natural Park (created in 1976) to the adjacent marine area. PMLS remained without a management plan until 2005, when zoning and management measures entered into force (Resolução do Conselho de Ministros no141/2005, 2005).

Figure 2.1- Panoramic of Serra da Arrábida [between 1957 and 1961] © Acervo fotográfico de Artur Pastor | Arquivo Municipal de Lisboa.

Arrábida MPA includes rocky coast and adjacent sandy substrates between Cape Espichel and Portinho da Arrábida. It has an area of 53 km^2 along a 38 km coastline of the Setúbal Peninsula, distributed along a strip oriented along the coast to a maximum depth of 100 m. In the extreme west of the park, bathymetry descends from the coast to the limit of the protected area, regularly reaching maximum depths of 40 m. On the south coast, the Park has a flat but steeper platform, up to 40 m, followed by a slope that reaches depths of up to 120 m in the Cabo Espichel area. The maximum depths gradually decrease from west to east, up to 60 m to 7 m before the easternmost complementary protection zone (Cunha et al., 2014; Henriques et al., 2013; Horta e Costa et al., 2013a). Arrábida MPA is managed by the Instituto da Conservação da Natureza e das Florestas (ICNF) and is included in the Natura 2000 Network of conservation zones (Arrábida/Espichel Site of Community Importance).

Arrábida MPA environment is extremely homogeneous and characterized as warm temperate. After a minimum in winter, with average values of 13°C, the temperature of surface water rises to 20°C in late spring and then decreases to 15°C in early summer, as a result of the coastal upwelling with the surface water moving outwards and replacement by cooler bottom water bodies. From September onwards, the more irregular wind regime does not allow the maintenance of the coastal upwelling, which leads to the water temperature approaching normal values for the season. The area is fundamentally under the influence of the North Atlantic current, which flows from north to south along the mainland coast. This region is also influenced by the presence of the deep Mediterranean current, due to the approach to the coast, induced by the existence of the submarine cannons of Setúbal, to the south and of Lisbon, to the west. On the other hand, given the proximity of the Sado river estuary, there is a marked influence of strong tidal currents, parallel to the coast, which continuously interact with the marine communities and habitats present. The salinity values in the zone, measured between 35 m and 45 m in depth, typically range from 35.55 to 36.20 (Horta e Costa et al., 2013b).

This MPA was established in order to protect a unique marine ecosystem and its natural resources from the impacts caused by various socioeconomic activities (Henriques et al., 2013; Stratoudakis et al., 2015). The area is protected from the action of the predominant North wind by Arrábida's mountains, which minimizes exposure to the waves, it is also in the vicinity of Sado estuary and of areas of abyssal canyons that create conditions for the great productivity of this area. In this context, we can find various habitats, from rocky reefs, kelp forests, seagrass beds and sand banks. The rocky reefs are where most biodiversity is concentrated as a result of the high complexity of macro and microhabitats, which in turn support many species of algae, invertebrates, and fish and where the reproduction and growth of many species of commercial interest occur (with a great abundance of larval and juvenile states of a significant number of species) (Cunha et al., 2014). Underwater rocky habitats of Arrábida MPA are highly heterogeneous and complex, resulting from the disintegration of limestone cliffs) (Gonçalves et al., 2002). All these characteristics make the area an important diversity hotspot for the biogeographic region (Gonçalves et al., 2002) with more than 1800 species of marine flora and fauna registered (Horta e Costa et al., 2013a; Cunha et al., 2014). The marine flora has floristic elements from the various divisions of the algae: forests of brown algae of the family of Laminaria, such as *Saccorhiza polyschides*; extensive forests of the genus Treptacantha, such as *Treptacantha usneoides*; underwater seagrass *Zostera marina* and encrusting algae populations *Mesophyllum lichenoides*.

Arrábida MPA is divided into eight zones with variable regulations (Resolução do Conselho de Ministros nº141/2005, 2005) ranging from total protected zones to complementary protection zones. The total-protected zone (TPZ) has 4 km^2; all the 4 partial-protected zones (PPZ) totaling 21 km^2; and the 3 complementary zones (CPZ) totaling 28 km^2. The TPZ is a no-take, no-go area (with the exception of research, monitoring, and education purposes). In the PPZ local commercial fishing with traps and lines is allowed beyond 200 m from shore, and no extractive recreational activities are permitted. In the CPZ, fishing vessels <7 m in length and recreational fishing are allowed. Commercial fishing licenses for the park were allocated only to fishers from Sesimbra. Commercial diving for bivalves or other marine organisms, spearfishing, trawling and purse seine netting are forbidden in all the MPA.

2.2 Data Sampling

The present study involves a type of random sampling, where any area of the studied location is equally likely to be sampled and, consequently, all individuals in the population are equally likely to be selected for the sample. Four sites with similar habitat structure, between 5 and 10 m depth, were sampled in November 2020: two within total protection zone (T1, T2) and two on complementary protection zone (C1, C2) to ensure spatial diversity (Figure 2.2).

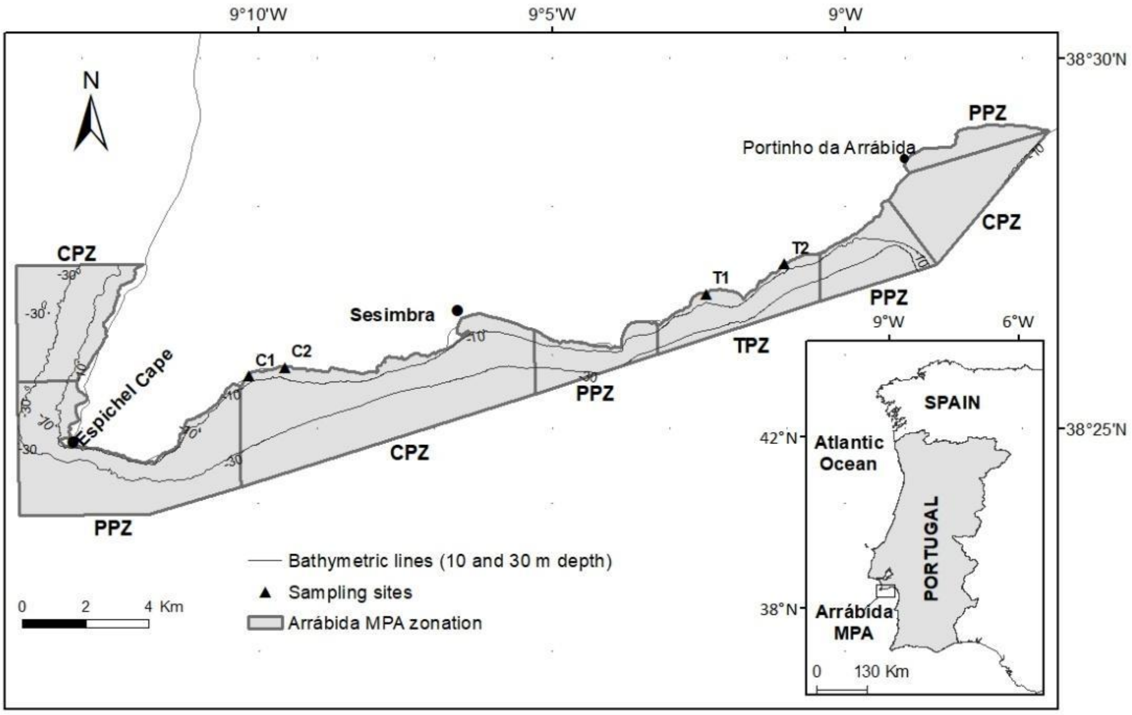

Figure 2.2- Marine protected area of Arrábida with designation of existing protection zones (CPZ- Complementary Protection Zones, PPZ- Partial Protection Zones, TPZ- Total Protection Zone) and sites sampled (C1, C2, T1, T2) in the study.

At each of the four sites, the HFS sampled were the most abundant in November 2020: *Halopteris scoparia* (Linnaeus) Sauvageau, 1904; *Saccorhiza polyschides* (Lightfoot) Batters, 1902; *Sphaerococcus coronopifolius* Stackhouse, 1797; *Treptacantha usneoides* (Linnaeus) Orellana & Sansón, 2019. Three replicates of each of the macroalgae species were randomly collected from each of the selected sites, except in T2 where *Saccorhiza polyschides* was not detected. Other variables related to the environmental conditions of each analyzed site were also collected by the divers (mentioned in detail below). HFS and associated fauna were collected by SCUBA divers, who swiftly enclosed macroalgae within a 500µm mesh bag, followed by removal of the algae holdfast from the rock substrate (avoiding collecting sediment from the substrate). After collection, samples were immediately wrapped in plastic bags containing water from the environment to prevent individuals from escaping. The plastic bags were placed in insulated containers (in dark) with artificial ventilation during transport to the laboratory.

2.3 Laboratory processing

2.3.1 Invertebrate processing

In the laboratory, samples were processed within 3 hours after collection, where each plant was carefully removed from the bag, being washed with salt water to facilitate the extraction of macrofauna. This process was accompanied using a ø200/203mm mesh sieve to avoid the loss of biological material. The collected organisms were stored in labeled plastic vials, being stored in 70% ethanol to preserve the long-term biological material. In a second screening, with the support of a binocular magnifier, all the macrofauna collected was separated from residues or epiphytic algae. The identification of organisms was conducted with the help of literature and several online databases, namely Alvarez, 1968; Chapman, 2007; Hayward & Ryland, 2017; Lecroy, 2000; Lincoln, 1979; Ruffo, 1989a, 1989b, 1989c, 1998; the

"Marine Species Identification Portal"; BOLD ("The Barcode of Life Data Systems") and WORMS ("World Register of Marine Species"). All individuals were identified to the lowest taxonomic level possible. All scientific names were confirmed or updated using the WoRMS database (http://www.marinespecies.org/).

2.3.2 Habitat-forming species (HFS) processing

After separating the invertebrates from the algae, each macroalgae was spread over a white background, slightly compressed, and photographed. Each of the macroalgae was weighed to obtain the wet weight - referring to the algal weight after the removal of excess water (20 minutes on paper towels) present in the fronds - and dry weight - final dry weight values were recorded when obtaining constant values after consecutive weighings (values obtained after drying in a drying oven at 60ºC) - to determine its biomass. The photographs were analyzed using ImageJ software. Each photo was converted to a TIFF format image, which was then transferred to a gray scale, producing a black and white binary image, for the calculation of fractal dimensions. Two morphological attributes of the thallus were obtained, following Chemello & Milazzo (2002), the algal height - measure from the base of the holdfast to the distal tip of the frond - and algal width - calculated from the maximum transverse distance across the primary branch (the largest one).

2.4 Functional diversity

Different traits can describe distinct aspects of ecological functions and the type of trait included in the statistical analyses might influence the mode assemblages are viewed (Bremner et al., 2006). In this study traits were selected to cover the main distinguishable features of benthic invertebrates (Martini et al., 2021; Wong & Dowd, 2015). Redundant variables based on Pearson´s correlations (i.e. r ≥ |0,90|; Figure B1 in appendix B) were removed from the analysis. Trait assignment resulted in seven categories of morpho-physiological and behavioral characteristics that could potentially affect the distribution and occurrence of these species: potential size; diet; feeding mode; adult life habit; adult movement; degree of attachment and sociability (Table 2.1). Information on the functional traits of species was obtained by consulting a variety of sources including primary and secondary literature, such as EOL ("Encyclopedia of life"); MarLIN ("The Marine Life Information Network")/BIOTIC ("Biological Traits Information Catalogue"); WORMS ("World Register of Marine Species"), and books such as "Lifestyles and Feeding Biology" by Thiel and Watling (2015) and from publications such as Cummins et al. (2005); Pearce et al. (2008) and Guerra-García et al. (2014).

2.5 Environmental analysis

Environmental variables could not be associated with an individual HFS, so they were aggregated and represented by an average value per site. Six environmental variables were collected to characterize each site. These variables were chosen since they could expectedly have an influence in macroinvertebrate distribution patterns observed. The variables analyzed were: structural complexity, number of refuges per size category (5-15cm/15-50cm/>50cm), mean depth, coast exposure, density of *Saccorhiza polyschides* and *Treptacantha usneoides* and percentage of algal coverage based on functional groups (Thick-Leathery Algae; Jointed-Calcareous Algae; Coarsely-Branched Algae; Encrusting Algae; Sheet Algae; Filamentous Algae) (Table 2.2). Redundant variables based on Pearson´s correlations (i.e. r ≥ |0,90|; Figure B2 in appendix B) were removed from the analysis.

Table 2.1- Functional traits of the epifauna sampled: potential size, diet, feeding mode, adult life habit, adult movement, degree of attachment and sociability. Invertebrate taxa were classified based on available literature and online databases (Table A1 in appendix A).

Biological Trait	***Categories***	***Description***	***Relevance***
Potential size	Very Small (<2cm) Small (2-5cm) Small–medium (5-10cm) Medium (10-15cm) Medium–large (15-30cm) Large (30-50cm) Very Large (>50cm)	Maximum body size as adult given in centimeters, as individual excluding appendages	Reflects the position of the species in the food web. Growth rate, productivity, metabolism, feeding interactions
Diet	Omnivores	Feeds on mixed diet of plant and animal material	Dietary habits of benthic invertebrates is pivotal to the studies of food webs and energy flows in marine ecosystems
	Herbivores	Feeds on plants	
	Macrocarnivores	Feeds on macro invertebrates and vertebrates	
	Microcarnivores	Feeds on micro invertebrates	
	Detritivores	Feeds on detritus	
Feeding mode	Suspension-feeders	Feeds by straing suspended matter and food particles from water	Impacts resource utilization and facilitation. Affects the depth of oxygen and detritus penetration and can enhance organic matter decomposition. Control of other species in the assemblage
	Carrion-feeders	Feeds partly or wholly on the bodies of dead animals	
	Deposit-feeders	Feeds on detritus that have settled on the bottom	
	Grazer	Active removal of organic material from macroalgae surface	
	Parasite	Organism that lives in or on another living organism, from which it obtains food and other requirements	
	Predator	Feeds by preying on other organisms	
Adult life habit	Domicolous	Species that build tubes	Living environment; foraging mode
	Fossorial	Species that burrow	
	Interstitial	Species that live in the interstices between grains of sand/macroalgae	
	Epi-/endozoic or epi-/endophytic	Living on or in other organisms	
Adult movement	Sessile	No movement as adult	Indicates the dispersal and recolonization potential and the invasiveness of an organism. Mobility, dispersal, ability to escape predation
	Swimmer	Movement above the sediment	
	Crawler	An organism that moves along on the substratum via movements of its legs, appendages, or muscles	
	Burrower	Movement in the sediment	
Degree of attachment	None Temporary Permanent	Individual level of attachment for shelter and feeding	Influences metabolic requirements and thus production and trophic support
Sociability	Solitary	Single individual	Social behavior
	Gregarious	Single individuals forming groups, growing in clusters	
	Colonial	Living in permanent colonies	

Table 2.2- List of environmental variables (habitat and biotic cover) measured at each of the four sites sampled in Arrábida MPA. Methods used to characterize variables described above. (*) Trait categories removed from the analysis because of redundancy.

Category	***Environmental variables***	***Measuring Methods***	***Relevance***	***References***
Habitat	Structural complexity	Combined topography index (CTI) that uses the "chain and tape" method (substrate rugosity index) in the field and another two topographic features (Pais et al., 2013). The depth of the deepest (Dd) and shallowest (Ds) points were recorded in meters. A diver puts on the lead rope and counts the number of upwards (Nu) and downwards (Nd), in a transect with a length of 25 m and three replicates each. Also calculated the linear distance (Ld) and stretched length (Lc). The first being obtained by the distance from the anchor point to the end of the leaded rope, and the second is the stretched length of the leaded rope $CTI = (1 - SR) + NC/25 + MVR/25$ ($SR = Ld/Lc$; $NC = (Nu + Nd)/2$; $MVC = Dd - Ds$)	Substrate architecture, referring to the planes and angles that make up the studied area, help to create heterogeneity and unique characteristics to maintain high biodiversity. Creation of micro-habitats that promote species coexistence	(Henriques et al., 2013; Kovalenko et al., 2012; Mazzuco et al., 2020; Tokeshi & Arakaki, 2012)
Habitat Habitat Habitat	Number of refuges (5-15cm) Number of refuges (15-50cm) * Number of refuges (>50cm) *	At each site a diver covered a 25 m transect, in the last 5 m of this the number of topographic elements of the rock substrate was identified and counted (i.e. cracks, crevices, caves and holes), then categorized by size categories	Presence of topographic elements that can increase or decrease the number of microhabitats in a given area, affecting the composition and abundance of organisms present. Shelter provision	(Kovalenko et al., 2012; Tokeshi & Arakaki, 2012; Tuya et al., 2011b)
Habitat	Mean depth (m)	Each analyzed depth was measured using the dive computer	Adaptation and alteration of existing communities with depth variation, related to codependent factors such as solar penetration, concentration of oxygen present, etc.	(Rosenberg, 1995; Satyam & Thiruchitrambalam, 2018)
Habitat	Coast exposure *	Based on the literature by Burrows et al. 2008, coastal exposure was measured using a digital coastline dataset for the region of interest (NOAA; available at: www.ngdc.noaa.gov/mgg/shorelines/gshhs.html)	Wave action (protected surfaces or exposed surfaces)	(Burrows et al., 2008; Satyam & Thiruchitrambalam, 2018)
Biotic Biotic	Density of *Saccorhiza polyschides* (N/m^2) Density of *Treptacantha usneoides* (N/m^2)	Represented by the holdfast number per 1m^2. Visual census carried out. Analyzed through three quadrants of 1x1 m each at every site	Dominant macroalgae in each studied zone may influence the composition of the macroinvertebrate community of the surrounding HFS, where the presence of organisms that prefer certain types of surfaces to live is verified	(Teagle & Smale, 2018)
Biotic Biotic Biotic Biotic Biotic Biotic	Thick-Leathery Algae (%) Jointed-Calcareous Algae (%) Coarsely-Branched Algae (%) Encrusting Algae (%) Sheet Algae (%) Filamentous Algae (%)	Macroalgae cover characterized by the number and nature of substrates. Photo analysis using the PhotoQuad program of 50x50 cm quadrants. Six categories defined according to functional groups defined by Littler and Littler (1984) and Steneck and Dethier (1994). Thick-Leathery Group (thick blades and branches, texture like leathery-rubbery); Jointed-Calcareous Group (articulated, calcareous macroalgae, with stony texture); Coarsely-Branched Group (coarsely branched, with fleshy-wiry texture); Encrusting Group (encrusting, epilithic, with a tough texture); Sheet-Group (sheet like, foliose with a soft texture) and Filamentous Group (delicately branched, with a soft texture, filamentous)	Macroalgal cover heterogeneity within the studied habitats affects the multivariate structure of organisms that cohabit in this area.	(Littler & Littler, 1984; Steneck & Dethier, 1994; Teagle & Smale, 2018)

2.6 Statistical analysis

In this study, aiming to assess the taxonomic and functional diversity of macroinvertebrates in each sample, two matrices were assembled. For taxonomic analysis, taxa were analyzed based on their abundance per host (HFS). For the functional analysis, we started from a point of view of proportions of each functional category, to analyze the dominance of traits per host. Variability in macroinvertebrate assemblage structure was examined using a two-factor PERMANOVA using type III sums of squares (Anderson et al., 2008), with the model comprising the factors site (random, 4 levels – C1, C2, T1, T2.) and HFS (fixed, 4 levels – *H. scoparia*, *S. coronopifolius*, *S. polyschides*, *T. usneoides*). Post-hoc pairwise tests were performed wherever significant differences were detected ($p < 0.05$), p-values were based on the Monte Carlo method (Anderson et al., 2008). PERMDISP routine was performed before running the PERMANOVA tests. Permutations (9,999 under a reduced model) were based on a Bray–Curtis similarity matrix on fourth root transformed data for the analysis with taxa abundances, and Euclidean distance matrix on untransformed data for the analysis with functional trait proportions. SIMPER (Similarity Percentages - species contributions) analysis was also carried out. SIMPER identifies the taxa's/traits that are most responsible for the observed patterns (e.g., responsible for typifying each level of a factor and those that contribute the most to the dissimilarity between levels) by disaggregating the similarities between samples. For the SIMPER analysis made from the bray-Curtis matrix, the more abundant a taxa is within a group, the more it contributes to the intra-group similarity, while a taxa with a consistently high contribution to the dissimilarity between groups is a good discriminating taxa (Clarke & Warwick, 2001). For the SIMPER analysis based on functional traits, Euclidean distances were used.

An unconstrained Principal Coordinates Analysis (PCO) was done, the result of a PCO is a set of coordinates on several derived axes such that similar cases are close together, helping to visualize the association patterns of the analyzed group. For the vector overlay showing HFS variables with vectors, the correlations with canonical axes are only shown when Spearman's rs > |0.5| in taxonomic analysis and Pearson's rs > |0.5| in functional analysis. A representation with taxa (Spearman's rs > |0.6) and functional traits (Pearson rs > |0.6) in vectors was also performed to see if there is any association with the HFS. A distance-based linear model (DISTLM) (Anderson et al., 2008) with BEST regression as selection procedure, using Akaike Information Criterion (AIC) (Mcardle & Anderson, 2001), was used to investigate the relationships between the invertebrates community and its possible predictors. The DistLM enabled us identify variables (on the normalized scale) that contributed significantly to the patterns observed in the assemblage structure as well as determine how much variation was explained by each variable. Before the DISTLM models were run, the existence of highly correlated variables and any need for data transformation was assessed using a draftsman plot. The results of the DISTLM analysis, illustrate using the redundancy analysis dbRDA method (Legendre & Anderson, 1999), emphasize the vectors that correspond to the variables selected in the best model. The length and direction of the vectors indicate strength and direction of the relationship. The HFS variables were based on Euclidean distance matrices, normalized with an average value of 0 and a standard deviation of 1, thus decreasing the impact of different measuring units in posterior analysis. Multivariate analyses were undertaken using the PRIMER (v6) software package (Clarke & Warwick, 2001) with the PERMANOVA add on (Anderson et al., 2008; Clarke & Gorley, 2006).

3. Results

3.1 Habitat characterization

Regarding HFS structure, the *Saccorhiza polyschides* species presented the highest values recorded in relation to all algal attributes measured, where its large dimensions stand out (Table 3.1), being responsible for the formation of large underwater forests in various parts of the globe. Contrarily, the HFS that registered the lowest values were *Halopteris scoparia*, standing out however for having elevated values of fractal perimeter and area (Table 3.1), responsible for high values of heterogeneity and microhabitats. For *Treptacantha usneoides* and *Sphaerococcus coronopifolius*, intermediate values were obtained, with *T. usneoides* the second largest measured HFS and *S. coronopifolius* the second HFS with the highest fractal values recorded (Table 3.1). The sites studied in the complementary zone are dominated by a higher density of macroalgae *S. polyschides*, having on average a higher presence of jointed-calcareous algae and greater depth (Table 3.2). The number of refuges available in the complementary protection zone are characterized by being of smaller dimensions and, on average, these sites have a smaller number of refuges when compared to the total protection zone (Table 3.2). In contrast, for the sites in the total protection zone, we have the presence of more refuges with larger average dimensions and a high density of *T. usneoides*, and an algal cover composed of more encrusting algae, with the sites on average being shallower (Table 3.2).

Table 3.1- Mean values (±SD) of macroalgal variables of the four HFS sampled at Arrábida MPA.

Macroalgal variables	*Treptacantha usneoides*	*Halopteris scoparia*	*Sphaerococcus coronopifolius*	*Saccorhiza polyschides*
Biomass per plant (dry weight in g)	32.46±23.69	1.88±0.74	10.06±8.22	70.26±42.83
Fractal area (cm^2)	79.18±30.68	56.68±15.20	96.38±37.59	97.59±26.77
Fractal perimeter (cm)	10 937.00±1 347.64	8 921.33±1 984.40	11 257.33±1 040.41	12 676.00±825.08
Height per plant (cm)	57.82±26.65	8.50±2.61	18.84±7.06	71.55±11.60
Width per plant (cm)	26.78±8.87	11.56±3.40	22.48±8.35	55.51±19.84

Table 3.2- Mean values (±SD) of the environmental variables of the four HFS sampled at Arrábida MPA. C1 and C2 sites are complementary protection zone; T1 and T2 sites are total protection zone.

Category	*Environmental variables*	*C1*	*C2*	*T1*	*T2*
Habitat	Structural complexity	0.34±0.00	0.55±0.00	0.45±0.00	0.45±0.00
Habitat	Number of refuges (5-15cm)	5.33±0.00	3.67±0.00	5.33±0.00	11,00±0.00
Habitat	Number of refuges (15-50cm)	2.00±0.00	1.67±0.00	6.33±0.00	15.33±0.00
Habitat	Number of refuges (>50cm)	0.00±0.00	2.67±0.00	1.33±0.00	2.33±0.00
Habitat	Mean depth (m)	6.23±0.00	5.05±0.00	4.32±0.00	6.68±0.00
Habitat	Coast exposure	671.05±0.00	1 077.03±0.00	1 203.50±0.00	1 002.41±0.00
Biotic	Density of *S. polyschides* (N/m^2)	8.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00
Biotic	Density of *T. usneoides* (N/m^2)	0.00±0.00	0.00±0.00	35.33±0.00	35.33±0.00
Biotic	Thick-Leathery Algae (%)	29.94±22.09	12.73±9.65	27.10±10.41	25.34±1.75
Biotic	Jointed-Calcareous Algae (%)	10.38±13.09	24.33±5.42	1.88±2.77	0.00±0.00
Biotic	Coarsely-Branched Algae (%)	4.70±1.39	4.59±4.43	1.83±0.42	2.11±1.87
Biotic	Encrusting Algae (%)	24.48±10.75	24.41±7.44	21.61±1.27	40.26±13.19
Biotic	Sheet Algae (%)	0.63±0.62	0.28±0.23	0.85±0.23	0.07±0.10
Biotic	Filamentous Algae (%)	2.74±1.86	3.98±1.82	8.36±2.94	0.00±0.00

3.2 Characterization of macroinvertebrates assemblages associated to habitat-forming species (HFS)

A total of 3,856 individuals were found, belonging to 182 different taxa encompassing eight phyla: Annelida, Arthropoda, Chordata, Echinodermata, Mollusca, Nematoda, Nemertea and Platyhelminthes (Table A2). The most diverse and abundant phylum was Arthropoda, comprising 50% of the total abundance and 103 different taxa, followed by Mollusca (31% of the total abundance and 54 taxa) and Annelida (9% of the total abundance and 11 taxa) (Table A2). Chordata, Echinodermata, Nemertea, and Platyhelminthes comprised less than 0.5% of total abundance. While the percentage of taxa belonging to each phylum remained relatively constant among HFS, abundance patterns differed among HFS: Arthropoda constituted approximately more than 50% of total abundance on *T. usneoides* (N=403), *S. coronopifolius* (N=451), and *H. scoparia* (N=500) but Mollusca was the dominant phylum on *S. polyschides* (N=837) (Figure B3). This was mainly due to the high abundance of taxa Rissoidae (Table 3.3). Within Arthropoda, the most abundant taxa were the families Amphilochidae (11% of all arthropods; N=206) and Aoridae (9%; N=178) (amphipods). Concerning Mollusca, Rissoidae and Cerithiidae accounted for 37% and 12% of all moluscan abundance (N=441; N=144), respectively. The polychaetes belonging to Nereididae and Syllidae comprised 44% and 27% of all annelids (N=165; N=101) (Table 3.3). Nematoda remained identified only up to the phylum (N=231).

General results by HFS, revealed that *S. polyschides* stood out both in number of individuals (N=1811) and in number of taxa present (T=134). *T. usneoides* showed the lowest abundances (N=616), while *H. scoparia* showed the lower diversity of taxa (T=63) (Table A2). Arthropods had an equitable distribution across the different HFS. At the opposite extreme, of the 1194 mollusc specimens, 837 were collected in *S. polyschides*. Throughout the study, some taxa were only recorded in one HFS. *Amphilochus manudens* (N=20) was just collected in *T. usneoides*; *Stenothoe spp*. (N=22) was just registered in *S. coronopifolius*; and Cerithiidae (N=144) only occurred in *S. polyschides*. The taxa Ammotheidae was found mostly associated with *H. scoparia* (67 individuals out of 73 collected).

From functional traits analysis, using the proportion of each functional category along the HFS collected in the study, a high dominance of individuals with small (2-5cm) and very small (<2cm) potential sizes (46.19%; and 38.28%, respectively). High proportions of omnivores (25.13%) and detritivores and/or herbivores (26.19%) were also found, predominantly feeding on detritus that have settled on the ground and plants (grazers) (28.84%). Most of the organisms identified have “solitary” behavior (49.07%), being “crawler” (45.57%) and inhabits “Interstitial” habitat, i.e., the spaces between individual sand grains or in HFS (63.9%) not living associated with any organism or substrate temporarily or permanently (Table 3.4; Figure B4). However, among the analyzed HFS, some patterns do not follow this trend. *H. scoparia*, also has a high dominance of microcarnivores and individuals with predatory characteristics, besides the high proportion of omnivores. *S. polyschides* epifauna is dominated by gregarious and shelters individuals with larger potential sizes than the other HFS (Table 3.4; Figure B4).

Table 3.3- List of most abundant taxonomic groups (N>200) with the five most abundant invertebrates' taxa, in each HFS collected (across all the four sites) in the Arrábida MPA, with total abundances (N total). Full table available in appendix A (Table A2).

Phylum	*Taxa*	*Treptacantha usneoides*	*Halopteris scoparia*	*Sphaerococcus coronopifolius*	*Saccorhiza polyschides*	*N (Total)*
Annelida		45	52	47	228	372
Annelida	Capitellidae	-	2	1	7	10
Annelida	Nereididae	6	4	1	154	165
Annelida	Sabellidae	25	23	14	5	67
Annelida	Serpulidae	4	1	-	11	16
Annelida	Syllidae	9	21	27	44	101
Arthropoda		403	500	451	573	1927
Arthropoda	Amphilochidae	32	17	155	2	206
Arthropoda	Amphipoda	11	87	17	9	124
Arthropoda	Aoridae	2	95	20	61	178
Arthropoda	Photidae	23	28	4	46	101
Arthropoda	Stenothoidae	37	30	27	18	112
Mollusca		84	106	167	837	1194
Mollusca	*Bittium reticulatum*	1	-	3	77	81
Mollusca	Cerithiidae	-	-	-	144	144
Mollusca	*Crisilla spp.*	-	-	23	62	85
Mollusca	Rissoidae	53	46	60	282	441
Mollusca	Trochidae	-	1	1	60	62
Nematoda	Nematoda	74	51	23	83	231

Table 3.4- Proportions (%) of functional traits categories in all epifauna found in each HFS along the sampled sites of the Arrábida MPA, Portugal in November 2020.

Functional Trait	*Category*	*Treptacantha usneoides*	*Halopteris scoparia*	*Sphaerococcus coronopifolius*	*Saccorhiza polyschides*	*% (Total)*
Adult Life Habit	Domicolous	8.77	7.98	2.94	5.52	6.02
	Domicolous/Fossorial	0.65	5.88	1.26	6.46	4.46
	Domicolous/Interstitial	2.27	14.71	2.80	5.69	6.28
	Epi-/endozoic or epi-/endophytic	14.94	9.94	6.43	7.07	8.74
	Fossorial	0.81	0.28	0.70	3.09	1.76
	Interstitial	68.34	46.36	80.42	62.78	63.90
	Interstitial/Fossorial	2.44	2.52	1.82	8.78	5.32
Adult movement	Burrower	2.44	5.32	2.52	6.96	5.11
	Burrower/Crawler	17.21	8.96	7.55	10.60	10.79
	Burrower/Swimmer	6.33	4.48	7.41	1.33	3.84
	Crawler	27.27	33.75	51.75	54.00	45.57
	Sessile	5.19	3.36	1.96	0.94	2.26
	Swimmer	23.70	7.42	13.29	2.54	8.82
	Swimmer/Crawler/Burrower	2.76	3.50	4.90	11.15	7.24
	Swimmer/Crawler	13.31	20.87	6.99	11.98	12.91
Degree of attachment	None	71.10	50.84	82.38	74.27	70.93
	Permanent	5.19	3.36	1.96	0.94	2.26
	Temporary	21.92	33.47	12.03	24.30	23.34
Diet	Detritivores	18.99	14.99	31.75	15.52	18.98
	Detritivores/Herbivores	12.34	14.99	17.20	38.87	26.19
	Detritivores/Microcarnivores	0.00	0.00	0.00	0.11	0.05
	Herbivores	12.01	2.52	4.48	5.85	5.96
	Herbivories/Detritivores/Omnivores/ Microcarnivores	2.44	3.50	3.92	10.99	6.92
	Herbivories/Omnivores	0.00	0.00	0.00	0.06	0.03
	Macrocarnivores	1.95	1.26	3.64	3.42	2.83
	Microcarnivores	8.93	18.49	12.73	4.69	9.41
	Omnivores	41.56	31.93	22.38	17.95	25.13

Table 3.4 (continued)

Functional Trait	***Category***	***Treptacantha usneoides***	***Halopteris scoparia***	***Sphaerococcus coronopifolius***	***Saccorhiza polyschides***	***% (Total)***
Feeding mode	Carrion-feeders	3.25	4.20	7.97	6.63	5.89
	Deposit-feeders	37.99	18.63	41.68	18.61	25.99
	Deposit-feeders/Grazer	22.40	16.11	20.00	39.54	28.84
	Suspension-feeders	6.33	3.64	5.31	5.85	5.42
	Grazer	3.08	1.54	2.80	5.52	3.89
	Parasite	2.60	2.66	2.94	2.37	2.57
	Predator	15.75	19.89	9.23	8.45	11.88
	Suspension/Deposit-feeders	6.82	21.01	6.15	10.44	11.02
Potential size	Very Small (<2cm)	36.85	43.84	49.79	32.03	38.28
	Small (2-5cm)	51.95	37.82	36.50	51.35	46.19
	Small–medium (5-10cm)	6.49	4.90	7.41	6.85	6.54
	Medium (10-15cm)	0.32	0.14	0.14	0.06	0.13
	Medium–large (15-30cm)	2.76	0.98	2.52	9.17	5.39
	Very Large (>50cm)	0.00	0.00	0.00	0.06	0.03
Sociability	Gregarious	37.18	35.15	23.78	49.86	40.27
	Solitary	50.65	49.72	48.25	48.59	49.07
	Solitary/Colonial	0.65	0.14	0.00	0.61	0.41
	Solitary/Gregarious	1.30	0.28	0.70	0.06	0.41

In the taxonomic analysis, PERMANOVA results confirm that macroinvertebrate assemblages´ composition differs between the studied HFS at taxa levels (Pseudo-F = 2.4155; $P < 0.05$). We also verified that the variation of the community was not only due to the studied HFS, but also to the dependence of the analyzed site. The interaction between HFS and sites was verified (Pseudo-F = 1.8692; $P < 0.05$) (Table 3.5). PERMDISP revealed significant differences in multivariate dispersions ($F = 5.0293$; $P < 0.05$). Besides, pairwise tests showed significant differences ($P(MC) < 0.05$) between *T. usneoides* and *H. scoparia* and *T. usneoides* and *S. polyschides* (Table 3.5; Table A3). Through the PCO analysis we were able to verify a separation of the epifaunal community. On the PCO1 axis there is a strong spatial separation of *S. polyschides* from the remaining HFS. On the PCO2 axis, it is *S. coronopifolius* and *S. polyschides* that separate from the remaining HFS in the sample space. When the correlation vectors were added, we found that 9 taxa and 2 predictor variables were strongly correlated ($\rho = 0.6$ and $\rho = 0.5$, respectively) with the distribution of HFS (Figure 3.1A). SIMPER results showed that *H. scoparia* have a more similar epifaunal assemblage (37.31%), while *S. coronopifolius* has a more variable community composition among replicates (22.53%) (Table A4). The Rissoidae characterizes all HFS, appearing as the main contributor to the analysis of similarity between groups of HFS. Comparisons between the different HFS showed that 35 taxa were responsible for approximately 50% of the dissimilarity between *S. coronopifolius* and *S. polyschides*, which are the most different algae in terms of macroinvertebrate community (82.43%), with the Nereididae family as the biggest contributor to this dissimilarity. On the other hand, *T. usneoides* and *H. scoparia* had the lowest dissimilarity in taxa composition (average dissimilarity of 71.54%) (Table 3.6), with the Aoridae family as the higher contributor to the dissimilarity (Table A5).

For the functional analysis, PERMANOVA results confirm that macroinvertebrate proportions differs between the studied HFS at functional traits levels (Pseudo-F = 2.4145; $P < 0.05$). The variation of the structure was not only due to the studied HFS, but also to the dependence of the analyzed site. The interaction between HFS and sites was also verified (Pseudo-F = 1.6406; $P < 0.05$) (Table 3.5). PERMDISP revealed no significant differences in multivariate dispersions ($F = 0.63146$; $P > 0.05$). Pairwise tests detected significant differences ($P(MC) < 0.05$) between *T. usneoides* and *S. coronopifolius,* and *S. coronopifolius* and *H. scoparia* (Table 3.5; Table A3). In the PCO analysis, *H.*

scoparia is further away from *S. coronopifolius* on the PCO1 axis, revealing functional differences, and *S. polyschides* is separated at the level of the PCO2 axis. When the correlation vectors were added, we found that 13 traits and 3 predictor variables were strongly correlated with the distribution of HFS (ρ = 0.6 and ρ = 0.5, respectively) (Figure 3.1B). In SIMPER results, *S. polyschides* presents itself as the HFS with the most similar functional categories in terms of proportion between itself, with an average squared distance of 0.36, while *T. usneoides*, *H. scoparia* and *S. coronopifolius* groups have similar values of average squared distance (0.43, 0.43 and 0.42, respectively) (Table A6). SIMPER revealed an average distance of 1.11 between *H. scoparia* and *S. coronopifolius* (the smaller the distance, the more similar the HFS), which were the most distant HFS in terms of traits structure, with 7 trait categories responsible for approximately 50% of this distance. Interstitial as adult life habit contributed the most to this difference (9.74%), followed by none as degree of attachment category (9.06%). *T. usneoides and S. coronopifolius* are the closest HFS groups in functional terms (average distance of 0.90) (Table 3.6), also with 7 trait categories responsible for approximately 50% of this distance. Deposit-feeders as feeding mode contributed the most to this difference (8.59%), followed by solitary as sociability category (8.33%) (Table A7).

Table 3.5- Results of multivariate permutational analyses of variance (PERMANOVA) for differences in macroinvertebrate assemblage structure in taxonomic and functional analysis, between sites (random) and HFS (fixed). The significance level was set to 0.05 (type III Sums of squares: 9999 permutations). Values indicated in bold are P-values < 0.05. Shaded areas denote significant results for pair-wise tests (P-values < 0.05).

Taxonomic PERMANOVA results			***Taxonomic pair-wise comparisons***					
Factor	**Pseudo- F**	**P(perm)**	***Tusne vs. Hscop***	***Tusne vs. Scoro***	***Tusne vs. Spoly***	***Hscop vs. Scoro***	***Hscop vs. Spoly***	***Scoro vs. Spoly***
Sites	4.2122	**0.0001**						
HFS	2.4155	**0.0001**	▨		▨			
Site×HFS	1.8692	**0.0001**						
Functional PERMANOVA results			***Functional pair-wise comparisons***					
Factor	**Pseudo- F**	**P(perm)**	***Tusne vs. Hscop***	***Tusne vs. Scoro***	***Tusne vs. Spoly***	***Hscop vs. Scoro***	***Hscop vs. Spoly***	***Scoro vs. Spoly***
Sites	4.5238	**0.0001**						
HFS	2.4105	**0.0134**		▨		▨		
Site×HFS	1.6406	**0.004**						

Table 3.6- Average between-group dissimilarities (%) and average squared distance between habitat-forming species (HFS) for the taxonomic composition and functional trait proportions of epifauna, respectively, as result of the SIMPER analysis.

HFS	***Taxonomic composition***	***Functional Trait proportions***
T. usneoides - H. scoparia	71.54	0.98
T. usneoides - S . coronopifolius	76.06	0.90
T. usneoides - S. polyschides	81.04	0.91
H. scoparia - S. coronopifolius	76.28	1.11
H. scoparia - S. polyschides	77.27	0.96
S. coronopifolius - S. polyschides	82.43	0.95

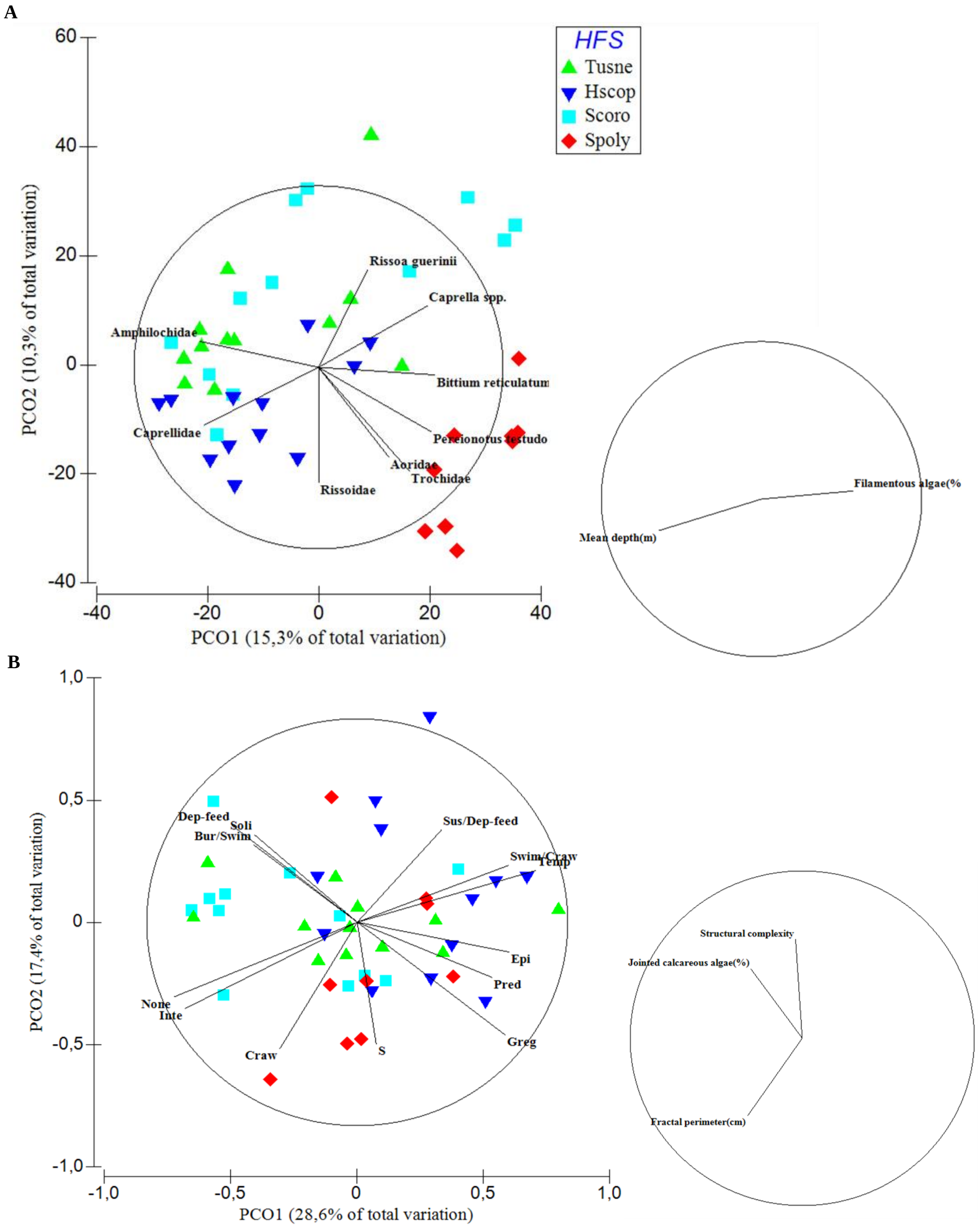

Figure 3.1- Principal Coordinates Ordination (PCO) plot of taxonomic (A) and functional traits composition (B) among HFS analyzed, based on Bray Curtis similarity and Euclidean distance resemblances matrixes, respectively. Vector length corresponds to the correlation (Spearman's rs > |0.6|) of a particular taxa and correlation (Pearson's rs > |0.6|) of a particular functional trait. Also shown in the bottom right is the equivalent ordination plot with the position of variables driving assemblages structure (macroalgal and environmental variables) (Spearman's rs > |0.5| and Pearson's rs > |0.5). Clockwise: Sus/Dep-feed- Suspension/Deposit-feeders in feeding mode category; Swim/Craw- Swimmer/Crawler in adult movement category; Temp- Temporary in degree of attachment category; Epi- Epi-/endozoic or epi-/endophytic in adult life habit category; Pred- Predator in feeding mode category; Greg-Gregarious in sociability category; S- Small (2-5cm) in potential size category; Craw-Crawler in adult movement category; Inte- Interstitial in adult life habit category; None- in degree of attachment category; Bur/Swim- Burrower/Swimmer in adult movement category; Dep-feed- Deposit-feeders in feeding mode category; Soli- Solitary in sociability category. Tusne- *Treptacantha usneoides*; Hscop- *Halopteris scoparia*; Scoro- *Sphaerococcus coronopifolius*; Spoly- *Saccorhiza polyschides*. Circles represent vector correlations of 1.

3.3 Variables driving assemblage structure

For taxonomic evaluation, the first two principal component axis of PCO explained 25.5% of community variability, the PCO1 axis explains about 15.3% and PCO2 axis explained about 10.3% (Figure 3.1A). From spearman's correlations (ρ = 0.5) between the variables (macroalgal and environmental variables) and the multivariate arrangement of the PCO, we verified that percentage of filamentous algae (ρ1 = 0.57) is related with positive values of PCO1, and that mean depth (ρ1 = -0.64) has a strong negative correlation with this axis. In PCO2 the correlations between the axis and the variables are weak, not being possible to associate any of the variables with the abundance of epifauna present in each HFS. In the multivariate multiple linear regression models (DISTLM) we found that the best model obtained was a model with three variables (AIC: 354.09), namely: mean depth, density of *T. usneoides* and width per plant (Figure 3.2A; Table 3.7) and explained up to 23% of the variation of the macrofaunal communities (Table 3.8). Other models were obtained, where the variables number of refuges with sizes between 5-15cm, structural complexity and density of *S. polyschides* were the only new variables added, the remaining variables being additions or subtractions of the chosen variables obtained for the best model.

For functional evaluation, the first two principal component axis explained 46.04% of traits variation (Figure 3.1B), the PCO1 axis explains about 28.6% and PCO2 axis explained about 17.4%. From Person's correlations (ρ = 0.5) between the variables (macroalgal and environmental variables) and the multivariate arrangement of the PCO, we verify that the variables that are related to the multivariate space were totally different from those obtained in the taxonomic analysis. Three variables were correlated. Fractal perimeter, jointed-calcareous algal cover and structural complexity were the variables with higher influence in the pattern observed (Person's ρ = 0.5). All three variables show a stronger correlation with PCO2 than with PCO1. In relation to PCO2, jointed-calcareous algal cover (ρ2 = 0.42) and structural complexity (ρ2 = 0.59) have a positive correlation with this axis and fractal perimeter (ρ2 = -0.46) has a negative relationship with it. In the multivariate multiple linear regression models (DISTLM) ten models were obtained, all with equal AIC values (AIC -40.045), meaning that any of them could be chosen to explain the variation of trait proportions. The best model selected includes five variables, namely: number of refugees (5-15cm), mean depth, density of *S. polyschides*, fractal perimeter and height per plant (Figure 3.2B, Table 3.7), that explained up to 31% of the functional variation (Table 3.8). In all the other models the only variables added were structural complexity and density of *T. usneoides.*

Table 3.7- Taxonomic and functional "weights" of chosen variables in each of the two axes that constitute the dbRDA plot.

Variable	***dbRDA1***	***dbRDA2***
Taxonomic Weights		
Mean depth (m)	-13.342	-7.8305
Density of *T. usneoides* (N/m^2)	2.4114	-12.152
Width per plant (cm)	10.369	-7.8894
Functional Weights		
Nº refuges (5-15cm)	-0.3731	0.1604
Mean depth (m)	0.3716	-0.1316
Density of *S.polyschides* (N/m^2)	-0.3005	-0.0322
Fractal perimeter (cm)	-0.0378	-0.2024
Height per plant (cm)	-0.0753	0.0782

Table 3.8 - Distance-based linear model (DistLM), with the representation of marginal tests and overall best solutions obtained based on the influence of variables driving assemblages structure, on the taxonomic and functional macroinvertebrate assemblage, using BEST selection procedure. % variation represents explained variation attributable to each variable added to the model. Values indicated in bold are P-values < 0.5

Taxonomic analysis

DistLM marginal test

Variable	*Predictors*	*Pseudo- F*	*P-value*	*% variation*
1	Structural complexity	2.0296	**0.0072**	4.51
2	Number of refuges (5-15cm)	3.4931	**0.0001**	7.51
3	Mean depth (m)	4.3897	**0.0001**	9.26
4	Density of *S. polyschides* (N/m^2)	2.0641	**0.0068**	4.58
5	Density of *T. usneoides* (N/m^2)	2.7771	**0.0005**	6.07
6	Thick-Leathery Algae (%)	0.84383	0.6563	1.92
7	Jointed-Calcareous Algae (%)	1.8552	**0.0166**	4.14
8	Coarsely-Branched Algae (%)	1.1322	0.2944	2.57
9	Encrusting Algae (%)	1.2689	0.1762	2.87
10	Sheet Algae (%)	1.4829	0.0808	3.33
11	Filamentous Algae (%)	3.0248	**0.0001**	6.57
12	Biomass per plant (dry weight in g)	3.0053	**0.0001**	6.53
13	Fractal area (cm^2)	1.4828	0.0751	3.33
14	Fractal perimeter (cm)	2.3215	**0.0015**	5.12
15	Height per plant (cm)	2.5508	**0.0005**	5.60
16	Width per plant (cm)	3.5823	**0.0001**	7.69

Overall best solutions

AIC	R^2	*RSS*	*No. Of Variables*	*Selections*
354.09	0.22857	98476	3	3;5;16
354.26	0.2257	98842	3	2;5;16
354.33	0.25814	94701	4	1;2;3;16
354.33	0.25814	94701	4	1;2;4;16
354.33	0.25814	94701	4	1;2;5;16
354.33	0.25814	94701	4	1;3;4;16
354.33	0.25814	94701	4	1;3;5;16
354.33	0.25814	94701	4	2;3;4;16
354.33	0.25814	94701	4	2;3;5;16
354.33	0.25814	94701	4	2;4;5;16

Functional analysis

DistLM marginal test

Variable	*Predictors*	*Pseudo- F*	*P-value*	*% variation*
1	Structural complexity	3.1307	**0.0035**	6.79
2	Number of refuges (5-15cm)	2.8719	**0.0074**	6.26
3	Mean depth (m)	1.0607	0.3621	2.41
4	Density of *S. polyschides* (N/m^2)	2.4074	**0.0208**	5.30
5	Density of *T. usneoides* (N/m^2)	4.2144	**0.0004**	8.93
6	Thick-Leathery Algae (%)	1.7468	0.0937	3.90
7	Jointed-Calcareous Algae (%)	3.4613	**0.0015**	7.45
8	Coarsely-Branched Algae (%)	2.0232	**0.0442**	4.49
9	Encrusting Algae (%)	0.87566	0.5147	2.00
10	Sheet Algae (%)	1.9026	0.0624	4.24
11	Filamentous Algae (%)	0.89143	0.5046	2.03
12	Biomass per plant (dry weight in g)	0.98468	0.4315	2.24
13	Fractal area (cm^2)	2.1321	0.0368	4.72
14	Fractal perimeter (cm)	3.6345	**0.0013**	7.79
15	Height per plant (cm)	1.8457	0.0679	4.12
16	Width per plant (cm)	2.1164	**0.0411**	4.69

Overall best solutions

AIC	R^2	*RSS*	*No. Of Variables*	*Selections*
-40.045	0.31338	14.156	5	2;3;4;14;15
-40.045	0.31338	14.156	6	1;2;4;5;14;15
-40.045	0.31338	14.156	5	1;2;3;14;15
-40.045	0.31338	14.156	5	1;2;5;14;15
-40.045	0.31338	14.156	5	1;3;4;14;15
-40.045	0.31338	14.156	5	2;3;5;14;15
-40.045	0.31338	14.156	5	2;4;5;14;15
-40.045	0.31338	14.156	5	3;4;5;14;15
-40.045	0.31338	14.156	6	1;2;3;4;14;15
-40.045	0.31338	14.156	6	1;2;3;5;14;15

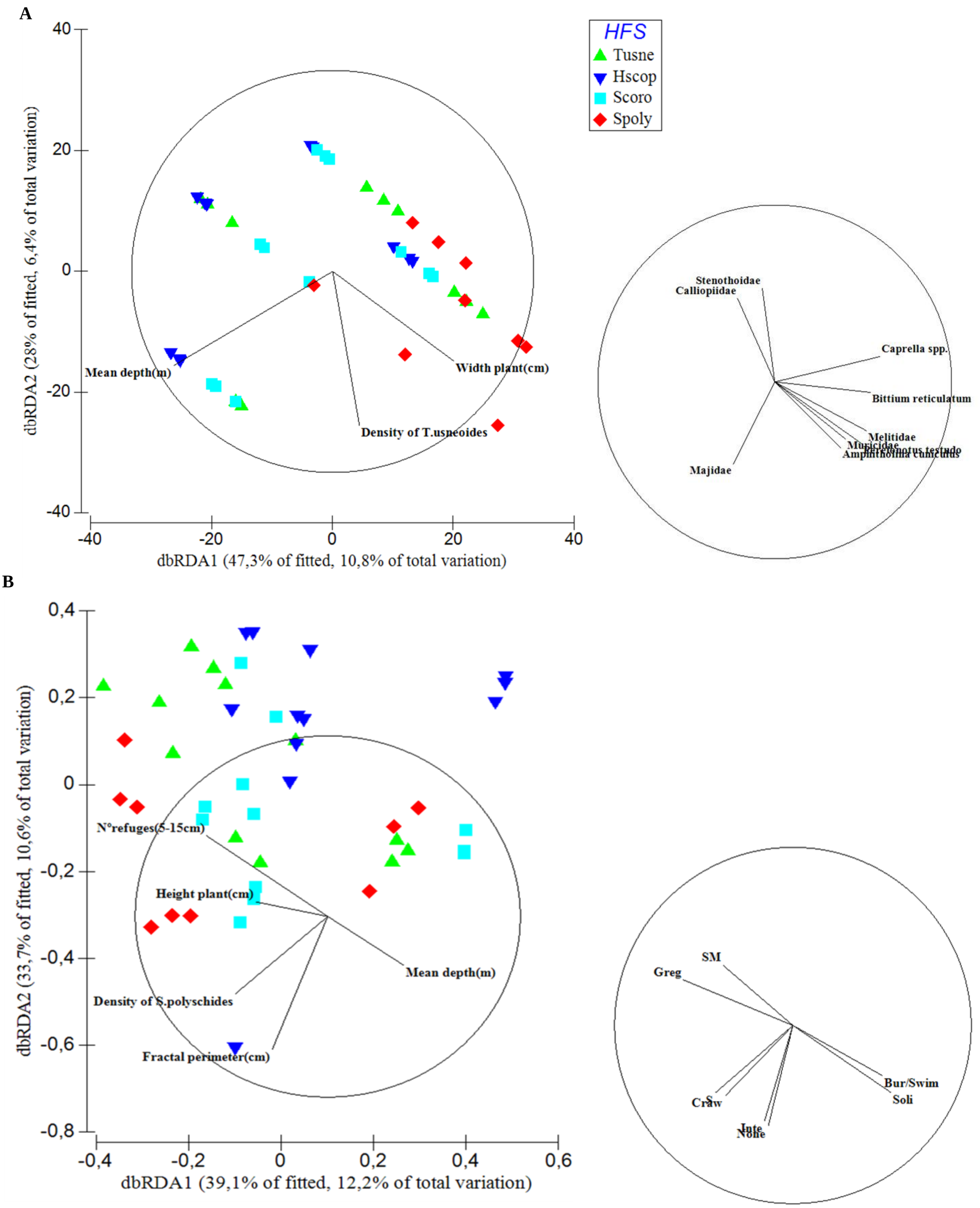

Figure 3.2- Distance-based redundancy analysis (dbRDA) plot to visualize DISTLM results in 2- dimensional space. Samples representation by taxonomic (A) abundance and functional (B) proportions, split into HSF species, overlaid with significant normalized variables. Also shown in the bottom right is the equivalent ordination plot with the position of taxa's and functional categories as vector driving assemblages structure (Spearman's rs > |0.5| and Pearson's rs > |0.5). Clockwise: SM- Small-medium (5-10cm) in potential size category; Bur/Swim- Burrower/Swimmer in adult movement category; Soli- Solitary in sociability category; None- in degree of attachment category; Inte- Interstitial in adult life habit category; Craw- Crawler in adult movement category; S- Small (2-5cm) in potential size category; Greg- Gregarious in sociability category. Tusne-*Treptacantha usneoides*; Hscop- *Halopteris scoparia*; Scoro- *Sphaerococcus coronopifolius*; Spoly- *Saccorhiza polyschides*. Axes show % of fitted and real variation of data cloud.

4. Discussion

This study highlighted the importance of macroalgae as habitat-forming species (HFS) in rocky reefs of Arrábida MPA, by describing the epifauna and highlighting the factors that drive the observed biodiversity patterns (i.e. taxonomic and functional dimensions), using information representative of habitat structure and complexity. In general, the results suggest that HFS species support an important diversity of macroinvertebrates, both in terms of number of taxa and abundance, and that the composition and functional structure of macrofaunal assemblages differ between each HFS. To our best knowledge, this is the first study, carried out in Portugal, that describes the functional structure of epifaunal assemblages associated with HFS in rocky reefs and their ecological relationships (i.e. links between the functional structure of both epifauna and HFS). The relationship between species composition and the respective functional traits variation of invertebrates remains poorly studied and understood in almost all types of marine habitats, as well as the effect of habitat structure on this variation (Beauchard et al., 2017; Bremner et al., 2006; Pais et al., 2014). In addition to taxonomic analysis, functional categorization of marine invertebrates is critically relevant, for the development of a better understanding of the biodiversity patterns and drivers of change, allowing the improvement of the current protection and restoration measures on temperate rocky reefs (Beauchard et al., 2017; Bustamante et al., 2014).

The epifauna patterns found in this study were taxonomically similar to others found in temperate rocky reefs worldwide, where crustaceans (particularly amphipods), molluscs and annelids dominate the assemblages (Navarro-Barranco et al., 2016, 2018; Sedano et al., 2020; Vázquez-Luis et al., 2009). The structure of the epifaunal community has long been known as being of special value in environmental studies on habitat and as an indicator of human pressures, as it undergoes great changes as a result of changes in the surrounding environment. Epifauna is environmentally sensitive to factors such as water quality and presence of macroalgae (Larson et al., 2022; Sánchez-Moyano et al., 2000b). The results showed that both HFS morphological variables and variables related to the surrounding habitat seems to drive the changes in the structure of epifaunal communities. An important observation is that the analysis by functional categories seems to be more efficient in analyzing patterns resulting from differences in the habitat structure that could go unnoticed only with the use of the relative taxonomic composition. Thus, the functional approach showed a better link between the predictor variables of habitat structure and invertebrates than the taxonomic approach. These results are consistent with other studies performed in rocky reef habitats, where the functional analysis proved to be an essential tool for analyzing the communities studied and their relationships with other communities and the surrounding environment (Henriques et al., 2013; Henseler et al., 2019). However, it should be emphasized that the taxonomic analysis in this study proved to be essential in the identification of specific associations. For instance, a preferential relationship has been found between *Amphilochus manudens* and *T. usneoides*, but, in general, the epifaunal assemblages were not specific to only one of the HFS which was also observed in other studies (Cebrián & Ballesteros, 2004; Navarro-Barranco et al., 2018; Silva et al., 2021).

On temperate rocky reefs most of the mobile epifauna live in association with macroalgae, that act as important habitat-forming species. Epifauna consumes a wide range of food items, being detritivorous, feeding on items available near the host (periphyton, algal epiphytes, other epifauna, plankton, etc.) and not on the host itself. Thus, most of the time, the epifauna does not show specificity with their prey items (Sánchez-Moyano & García-Gómez, 1998). Amphipods, as well as many of the epifaunal taxa, are demersal zooplankton that spends most of their time in the water column at night and resting during the day in the substrate (Bremner et al., 2006; Cacabelos et al., 2010; Guillemot et al., 2011; Navarro-Barranco et al., 2021; Russo, 1997), stopping in the host that is closest and available (Alldredge & King, 1980, 1985; Hammer, 1981; Taylor, 1997a). In this study Photidae and Stenothoidae are examples of taxa that demonstrate both a generalist distribution and diet.

Macroalgae have been recognized as key structural elements in marine ecosystems, adding physical complexity to the substrate and increase species diversity and richness (Bégin et al., 2004; Bué et al., 2020). Our results reveal that *Saccorhiza polyschides*, the HFS that recorded the highest values of macroalgae variables, also supported the greatest number of individuals and taxa. These individuals also have larger potential sizes, when compared with the epifauna of the remaining HFS. *S. polyschides* is a macroalgae common to several sublittoral zones of the Atlantic coasts of Europe, with thick blades and branches, and a leathery/rubbery texture, but the bulb is its most distinctive feature (McKenzie & Moore, 1981). The epifauna, which is found almost exclusively in the bulb, is distinct from the epifauna found in the remaining HFS analyzed. In all the remaining there is a dominance of arthropods, while in *S. polyschides* molluscs dominate the community. *Bittium reticulatum*, Trochidae and Nereididae were found almost exclusively associated with *S. polyschides* as well as Echinodermata. The bulb alone represents a set of five microenvironments, consisting of an outer layer, several invaginations that create spaces and where often two different bulbs can merge, a crevice between the bulb and the rocks, an internal cavity, and a large surface area of bulb wall (Norton, 1969) potentially available to burrowers. Here, specimens with domicolous and fossorial life habits dominate the assemblage. There is also a dominance of a less mobile, more permanent community, composed of consumers of decaying detrital material and herbivores, namelly gastropods and polychaetes with gregarious characteristics. Since our sampling took place in autumn (November), *S. polyschides* may have been favored when compared to other macroalgae that do not have the ability to stay on the substrate when faced with stronger currents and forming permanent communities, as this HFS has. Franco (2007) in the same geographical area, concluded that *S. polyschides* is the HFS that presents the largest biomass values in the autumn months when compared with the remaining macroalgae present. This is mainly due to the presence of the bulb, which makes the macroalgae remain fixed to the substrate during almost all seasons of the year (only being vestigial in winter) (Fernández, 2011). Additionally, the presence of high numbers of crustaceans from the Ampithoidae family, specifically *Amphitholina cuniculus*, were found. Ampithoids build their tubes from algal fragments and their normally brownish color favored their camouflage in a bulb background (Boeck, 1870; Burdette Barrett, 1966; Lowry & Myers, 2009; Skutch, 1926).

The existence of quantitative macroalgal studies and approaches, as well as the study of the influence of algal morphology on the hosts, may help to explain the abundance and potential epifaunal sizes found in this HFS. Russo (1997) observed the accumulation of greater numbers of individuals in algal mats with greater biomass and surface area, and Gunnill (1982) with a study on the effects of plant size and distribution on the number and size of invertebrates, inhabiting the brown alga *Silvetia compressa* in California (USA), concluded that larger plants generally harbor more and larger specimens than smaller plants. These quantitative approaches showed that biomass, height, and width are positively related to the surface area of the macroalgae, which in turn represents the available space for different species to live. Furthermore, host morphology can strongly influence epifauna abundance and species composition (Chemello & Milazzo, 2002; Edgar & Aoki, 1993; Navarro-Barranco et al., 2018; Russo, 1997). Tokeshi & Arakaki (2012) review the conceptual/theoretical basis for the multifaceted characteristics of habitat complexity, and in a more practical way Veiga et al. (2014b) studied two native and one invasive macroalgae species on two rocky shores in northern Portugal and highlighted the importance of applying fractal measurements in the study of complexity. The fractal area indicates how the perception of surface area can change with scale, being a measure of the space between sheets. The fractal perimeter indicates the complexity of the edge, relating the nature of the gaps between parts of the macroalgae, high values show additional division of space on smaller scales (McAbendroth et al., 2005).

Treptacantha usneoides recorded the lowest values of abundance and diversity of associated epifauna, while values for *Halopteris scoparia* and *Sphaerococcus coronopifolius* were similar. *T. usneoides* is a perennial HFS with a leathery consistency (Sadogurska et al., 2021), with a wide distribution in rocky substrates (Sales & Ballesteros, 2009), and attaches to the substrate by hapters or a fragile disc (García-Fernández & Bárbara, 2016). Besides have suffered a considerable regression process in the last decades, due to anthropogenic pressure (García-Fernández, 2020), is still an important HFS, both in this study and in the entire Mediterranean, where they are among the most productive communities, providing habitat to a considerable number of algae and invertebrates (García-Fernández, 2020; Orellana et al., 2019; Sales & Ballesteros, 2009; Verlaque et al., 2019). Despite being the HFS that offers the second largest amount of available habitat, its structure does not offer much space available for specimen protection (lower levels of fractal measurements), being even below *S. coronopifolius* which is much smaller in size but has higher structural complexity, with the second highest values of algal architecture (having both fractal area and fractal perimeter similar to *S. polyschides*) and abundance of macroinvertebrates registered. We assume that fractal measures seem to help explain the differences found in the analysis of assemblages. Moreover, longer fronds are more exposed to the beating of waves and, therefore present a more stressful substrate for the epibiont organisms (Paresque, 2008), so we hypothesize that other factors may also be relevant, namely the local hydrodynamics. Franco (2007) found that despite *T. usneoides* being constantly present in temperate rocky reefs, the biomass values were reduced, as this HFS in its winter form has only an erect thallus of reduced dimensions with the presence of epiphytic algae. Since our sampling occurred in late November (late autumn), natural hydrodynamics could have conditioned the epifauna association, probably making the structure and texture of *T. usneoides* less suitable for the presence of macroinvertebrates. Most of the epifauna found was in fact occupying other epiphytic algae that live in association with *T. usneoides*, which is in agreement with previous studies (Belegratis et al., 1999; Cacabelos et al., 2010; García-Fernández & Bárbara, 2016; Zheng et al., 2015). Epifauna associated with *T. usneoides* was dominated by arthropods and presents the lowest abundance of molluscs of all the studied HFS. Hacker & Steneck, (1990) manipulated the tenacity (related to the texture of the macroalgae, the ability to "cling") which had a positive effect on the number of amphipods present. Thus, the characteristics of the macroinvertebrate community reflect the resistance to currents and lack of shelter offered by this HFS, being generally composed of more mobile individuals, the specimens have appendages adapted to “cling” on macroalgae, walk, or swim actively, such as *Amphilochus manudens,* and the families Caprellidae and Sphaeromatidae (more specifically *Dynamene spp.*). Having raptorial appendages known as gnathopods, organisms swim by rapidly bending and straightening their bodies to move from one macroalgae to the other and rely on drag swimming powered to move around (Paresque, 2008). These organisms have generalist habits regarding diet and feeding mode, being omnivores, mostly feeding on detritus. A great abundance of individuals with gregarious and parasitic characteristics (such as Leucothoidae, which was only registered in *T. usneoides*), and phylum Nematoda (which appeared expressively in this HFS) were observed. Similarly to *S. polyschides*, individuals associated with *T. usneoides* have larger potential adult sizes (2 to 5cm). A relationship between the size and amount of habitat of the HFS and the size of the individuals seems to occur, with larger HFS associated to larger individuals and smaller HFS with smaller individuals.

S. coronopifolius and *T. usneoides* are the closest HFS groups in terms of epifaunal functional structure. *S. coronopifolius* is an erect HFS with flattened leaves, with a cartilaginous-membranous texture and a very branched structure, despite suffering a reduction in its size in the unfavorable season (autumn and winter), it manages to keep its disc and the first cylindrical branches present (Navarro-

Barranco et al., 2021). It produces a high amount of secondary metabolites acting as allelochemical deterrents (Navarro-Barranco et al., 2021; Quémener et al., 2021; Smyrniotopoulos et al., 2010), which may be the explanation for the low percentage of herbivores found, with macroinvertebrates feeding mostly on detritus that have settled on the bottom (Navarro-Barranco et al., 2021), as it happens for the family Amphilochidae, that showed a preferential association to this HFS. Among the herbivores present, S*tenothoe spp* stands out, which also seems to have a preferential association to *S. coronopifolius*, having a low sensitivity to secondary metabolites being well adapted to live in this type of host (Navarro-Barranco et al., 2021).

S. coronopifolius and *S. polyschides* are the most different HFS in terms of macroinvertebrate assemblages associated. *S. coronopifolius* has few individuals with a greater dependence on the host (as annelids and nematodes), and its community is mainly constituted by arthropods that live freely in the HFS, only depending on the deposition of detritus for their diet. Being a very branched HFS, with a membrane-like texture retaining in its fronds the detritus necessary for the feeding success of the associated macrofauna, as well as helping to retain and provide shelter for individuals who try to overcome the more aggressive hydrodynamic conditions present (Fratini et al., 2019). This HFS has a high potential to become an essentially important macroalgae for a more complete study of ecological networks. In a study by Franco (2007) carried out in the same geographical area, it was found that of the 11 species of macroalgae analyzed, this macroalgae revealed a constant presence over the months and showed the highest relative abundance values. Additionally, also registered greater number of associated juveniles fishes, having been used by all captured species. Seeming to be essential for the settlement and recruitment of juvenile fishes, it is also inevitably important for lower trophic levels, such as for the studied macroinvertebrates, which are the dominant food of these fish in the initial stages of life (Taylor, 1997a, 1998).

Although *H. scoparia* presents the lowest values recorded for all macroalgal variables, it is presented in this study as an HFS of high relevance, since it supports important levels of invertebrate diversity, both in abundance and number of taxa. *H. scoparia* generally distributed in the Atlantic Ocean, is erect and flexible, with a bushy-looking thallus, present all year in mainland Portugal (Patarra et al., 2017; Sánchez-Moyano et al., 2000b), being a much-ramified macroalgae. It is of high importance for the seaweed industry, as it has important antifungal, antibacterial and anti-aging properties (Patarra et al., 2017), and it is also an HFS with high ecological importance for epifauna, namely because it functions as food and direct refuge for various organisms (Chemello & Milazzo, 2002; Patarra et al., 2017; Sánchez-Moyano et al., 2000b). All morphological features of the HFS can help explain the high epifauna present, suggesting that the complexity of the algae is an important feature to consider. *H. scoparia* when buoyed up by water form inverted cone-shaped tufts with a very delicate appearance due to the many filamentous branches and a dense ramification with a high number of interstices (Sánchez-Moyano et al., 2000a), where, interstitial space creates a high availability of microhabitats (Hacker & Steneck, 1990), which retains lots of sediments and epiphytic algae, even in the presence of stronger currents. Most of the macroinvertebrates utilize the inter-vegetation gaps, when spaces between vegetation are smaller and more complex (Cacabelos et al., 2010; Kovalenko et al., 2012; McAbendroth et al., 2005; Tokeshi & Arakaki, 2012). Since hydrodynamics is considered one of the drivers of faunal composition in rocky reefs (Patarra et al., 2017), it is likely that it had an influence on the diversity patterns found. Strong currents and high wave action leads to an increase of coarse material accumulation, and coarse sediments tend to improve the abundance of the epifauna (Patarra et al., 2017). Therefore, it is not surprising that specific taxa preferred this HFS. For instance, the presence of sea spiders, more specifically the class Pycnogonida, a carnivorous and gregarious group of predators, was found between the filamentous branches. Being arthropods, they have an extremely reduced body and eight to twelve elongated legs, finding in the dense ramification a way to probably maintain themselves effortlessly within this HFS (Patarra et al., 2017; Sánchez-Moyano & García-Gómez, 1998). In agreement with other studies, other associations with high abundance of taxa were found, respectively crustacean belonging to Aoridae, Stenothoidae and Tanaididae, which have different feeding modes, with emphasis on suspension/deposit-feeders and predators. There is also an association with taxa with a higher degree of attachment, where the adult life habit is interstitial, burrower and domicolous/fossorial, respectively. Gastropod belonging to the Cingulopsidae family were also associated with *H. scoparia*. As already mentioned above, larger HFS also support individuals with larger potential sizes which agrees with the pattern found in this macroalgae of smaller dimensions, where very small size individuals dominate (i.e. taxa < 2cm) (Chemello & Milazzo, 2002; Sánchez-Moyano et al., 2000b).

Regarding the environmental variables, measured in the surrounding habitat, that could be contributing to the variations found among the HFS, a correlation was found between the number of small refuges, the density of *T. usneoides* and *S. polyschides* and the distribution of epifauna. This correlation is not surprising since the greater the number of micro-habitats created, the greater the heterogeneity and, consequently, higher levels of biodiversity are expected (Broyeri et al., 2001; Gray et al., 2006; Tokeshi & Arakaki, 2012). The density of the dominant macroalgae in the sampled sites, measured in terms of the number of holdfasts per m^2, proved to be important both in the functional (density of *S. polyschides*) and in the taxonomic analyses (density of *T. usneoides*). Differences in epifauna assemblages in terms of diversity found at each HFS may be related to the offer of other favorable microhabitats, since macroalgae with less structural complexity retain little sediment and organic matter between the fronds, and present lower values for species richness, abundance, diversity, and evenness than others more complex algae that inhabit the same local (Paresque, 2008). Micro-topographic features of substrates, such as the number of shelters (holes) per size category, relates to substrate architecture, apparently enhance complexity, affecting the distribution, abundance and variety of organisms present in habitats (Cacabelos et al., 2010; Kovalenko et al., 2012; Tokeshi & Arakaki, 2012). These structural characteristics offer physical shelter to reduce the effectiveness of predators, reducing their predatory effect on prey (as for example in the case of juvenile fish and invertebrates), offering more attractive niches for a wide variety of species (Leite et al., 2009). This importance was detected in coral reefs, explaining a large proportion of the variety found in fish abundance (C. Roberts & Ormond, 1987) as well as the recruitment and nesting characteristics of the species *Haliotis laevigata*. Also, many species of crustaceans seem to be limited by the shape and availability of shelters present in the substrate (Alexander et al., 2009). Thus, these environmental variables provide both shelter from predation, a broader surface from which to obtain food and more easily find a favorable substrate to resist displacement by wave action (Bruno et al., 2005). Mean depth measured at the time of sampling, were also related to the distribution and abundance of communities, both at taxonomic and functional levels. This finding agrees with previous studies showing significant differences in the structure of macroalgal assemblages in the Mediterranean, both in number and composition, when analyzed at different depths (Balata & Piazzi, 2008; Eriksson & Bergström, 2005). Franco (2007) in his study verified that *S. coronopifolius* is associated with depths from 4 meters onwards, while the species *T. usneoides* is associated with shallower depths. At the upper limits, the water level and wave action are essential to regulate communities. Habitats in deeper zones are characterized by environmental variables related to physiological constraints, being the substrates less disturbed, and containing more stable communities, as waves lose energy with depth, thus, it is essentially the available light that limits photosynthesis and the sediment cover that limits the areas available for recruitment (Balata & Piazzi, 2008; Guinda et al., 2012; Sangil et al., 2021; Win, 2011). In general, the decrease in light penetration limits the growth of macroalgae, and in-depth perennial algae of smaller sizes are found. Thus, a reduction in epifaunal abundance is expected, related to decreased water movement which leads to fewer food opportunities for filter-feeding species (Chemello & Milazzo, 2002) and reduced light levels which can lead to limiting micro algal food availability (Cusson & Bourget, 2005). However, in several studies carried out in the mediterranean the exactly opposite happens. There is an increase in the abundance of some species of juvenile fish and epifauna (where sessile individuals dominate), with an increase in taxa that have a preferential association with deeper and sheltered zones (Balata & Piazzi, 2008; Franco, 2007; Win, 2011) as is the case of the fish *Centrolabrus exoletus* and the arthropods *Ampithoe spp.* and *Monocorophium acherusicum* (Jacobucci, 2002). In relation to our study, we can hypothesize that the slightly deeper zones could have been important for a greater number of individuals, mainly as a refuge. However, future studies should be carried out (namely in the westernmost part of this AMP) to support this hypothesis, since all sites were analyzed at very superficial depths (up to 10m), requiring greater differences in depths to draw significant conclusions on the distribution of HFS and their associated epifauna.

Epifaunal communities are ecologically important as they are a fundamental and ubiquitous component of marine food webs, supporting the flow of energy through marine ecosystems and providing a unique link between benthic primary producers and consumers of higher trophic orders (Fulton et al., 2019; Larson et al., 2022; Milner et al., 2015; Paul et al., 2006; Sánchez-Moyano & García-Gómez, 1998; Sedano et al., 2020; Teagle & Smale, 2018). However they are often overlooked because the sample processing is time consuming and the identification of so diverse species from different taxonomic groups is very challenging (Fraser, 2020; Taylor, 1998). This processing is very meticulous and requires a high level of expertise to ensure correct identification to the species level (Navarro-Barranco et al., 2021). The large abundance of detritivores present in our study was mainly due to amphipods. This group is often the most abundant (more than 50%) of all the mobile fauna found in macroalgae (Edgar, 1983; Figueiredo, 2019; Gabr et al., 2020). Therefore, this study provides important information on these vagile assemblages that play a key role in trophic webs (Chen et al., 2021; Newcombe & Taylor, 2010), being an important component of the diet of large number fish (e.g. mediterranean labrids, blennids and trypterigids are very common and highly related to macroalgal-dominated communities) (Chemello & Milazzo, 2002; Guidetti et al., 2014; Harmelin-Vivien, 2000; Macpherson, 2000) and invertebrates of temperate rocky reefs. In addition to their importance for food webs, amphipods can also be considered as a valuable importance tool for the detection of anthropogenic impacts, being considered one of the most sensitive groups to environmental variations (De-la-Ossa-Carretero et al., 2012; Gesteira & Dauvin, 2000; Lee et al., 2005; Sedano et al., 2020).

Macroalgae as habitat-forming species in temperate rocky reefs are important areas of nursery for juvenile fishes in their settlement and recruitment phases (Franco, 2007; Taylor, 1997b), depending almost entirely on macroalgae epifauna for their food, their densities are directly affected and changed when prey density decreases (Franco, 2007; Fulton et al., 2019; Roff et al., 2013; Win, 2011). Navarro-Barranco et al. (2018) found that competitive displacement of *H. scoparia* might lead to a significant decline in the amount of food resources for many species that prey on epifaunal organisms and, in turn, to a bottom-up impact on higher trophic levels (cascading effects). A seasonal change in the abundance and distribution of HFS would be expected (Leite et al., 2009) as macroalgae are reduced to their minimum sizes in the late autumn and winter months, while their biomass peaks generally occur in the spring and summer (May-September) (Franco, 2007; Fraser, 2020). Therefore, in addition to the spatial analysis, carrying out a temporal analysis would be essential.

Further studies to quantify the origin of epifaunal variation should be made, namely, to determine to what extent the association between macroinvertebrates and macroalgae is driven by the morphology of the HFS surface and not by other characteristics (Dubiaski-Silva & Masunari, 1995; Hacker & Steneck, 1990; Lippert et al., 2001; Navarro-Barranco et al., 2021). One possibility could be the use of artificial macroalgae (plastic 'plants') similar in morphology to the natural macroalgae, to allow a more integrative study with stronger conclusions (Cacabelos et al., 2010; Gerrish & Bristow, 1979; Hansen et al., 2011; Taniguchi et al., 2003). Furthermore, it would also be important to include other architectural measures of the HFS, as degree of branching and stem width, which are measures that showed relevance in the distribution of the epifauna in other studies from temperate rocky reefs (Chemello & Milazzo, 2002; Edgar & Aoki, 1993; Fraser, 2020).

We conclude that the epifaunal community associated with macroalgae as HFS may vary according to the characteristics of their fronds and the environmental conditions of each location. Factors such as algal morphology and the ability to retain particles are important in regulating these communities (Chemello & Milazzo, 2002; Corte et al., 2012; Fraser, 2020). The sampled period implied that the study area was more exposed to the action of currents, where the HFS from deeper areas probably benefited, and there was HFS where only species that have a prehensile structure for attachment, such as strong gnathopods or some other physiological characteristic, manage to dominate. *T. usneoides* seemed to beat a “disadvantage”, with a greater abundance of individuals with appendages adapted to cling, walk, or swim actively. *S. polyschides* has individuals with potentially larger sizes, favoring the molluscs that are found in large numbers in the bulbs of these HFS. Although it harbors a considerably smaller fauna than other species of macroalgae with greater structural complexity, *H. scoparia* communities are of great ecological importance, probably due to its bushy texture with many interstitial spaces. In this context, the monitoring of the epifauna, such as arthropods, and the variations in the size, structure and area covered by macroalgae can be used as indicators of ecosystem health and, in this way, constitute a theme for future studies, optimizing information for a more complete and strong management of marine protected areas.

Final remarks

Marine biodiversity, recognized as an important supply of services and resources, is intrinsically driven to numerous biological (predation, recruitment, etc.), physical (tides, habitat structure, temperature, topographical heterogeneity, etc.) and chemical (salinity, nutrients, etc.) variables, which makes the task of analyzing their patterns so complex (Cusson & Bourget, 2005; Puente et al., 2017; Schneider & Mann, 1991; Vasconcelos et al., 2016). This study showed that both the variables related to the HFS morphology, and the variables related to the environment surrounding them, contributed to the variation observed in the structure of epifaunal communities. It would be important, at this stage, to extend the studies related to the characteristics of the HFS that are determinant for the variation in the epifaunal community found. Although a large set of predictor variables were included in this study, other variables such as macroalgae texture, color, and production of secondary metabolites, may also have an important role in the biodiversity patterns (Chemello & Milazzo, 2002; Huang et al., 2007; Lewis, 1987; Lippert et al., 2001). Thus, it would be important in future studies to include the use of artificial macroalgae that mimic natural macroalgae, helping to exclude other characteristics beyond algal morphology (Carreira-Flores et al., 2020; Edgar, 1991; Taniguchi et al., 2003). Other macroalgae measures could also be added to the analysis, helping to disentangle additional patterns or strongly support some of the patterns observed. Branching degree is an important measures of macroalgal complexity, thus being an important measure to be included in future studies. Generally speaking, the greater length of the secondary branches and the greater distance of the distal branches from the main stem provide greater interstitial cover for the epifauna to protect itself from possible predators (Chemello & Milazzo, 2002; Edgar & Aoki, 1993; Fraser, 2020; Lippert et al., 2001).

The recognition and characterization of macrofauna communities is an important process both for the assessment of biodiversity and for the assessment of the foundation of coastal ecosystems and their management and conservation. It is important to evaluate organisms from a taxonomic and functional point of view, as there has been an increasing presence of a biotic singularity and homogenization (Kovalenko et al., 2012; Navarro-Barranco et al., 2018), with altered systems. Where, a greater density of invasive species is present, being difficult to predict trophic changes that they can cause in a food webs (Navarro-Barranco et al., 2018). One of the key advances of this study was the assessment of both taxonomic and functional structure together, as this integration helps to explain not only the biodiversity patterns associated with these HFS but also their ecological relationships (i.e. links between the functional structure of the epifauna and the macroalgae), being a step forward to the understanding of HFS contribution for the rocky reefs functioning. The functional analysis performed in this study responded more effectively to community variation, reinforcing the need to include measures of life-history traits in future work that includes community analysis. Body size is offered as a measure capable of replacing niche measures of each species and, by extension, ecological networks. Since this study resorted to the use of potential sizes of the epifauna species, it would also provide more accurate results if we resorted to the calculation of the actual body sizes of individuals in future studies. Many life-history traits are related with body size and diet and their variation can have effects at various scales, from the individual to the ecosystem (Andersen et al., 2016; Woodward et al., 2005). The combination of body size and diet traits would be a way to better understand the biotic interactions between species in the future, namely trophic relationships. In future studies, the combination of these two traits could be a way to reduce a set of covariant species traits to a smaller dimension (Woodward et al., 2005).

It is expected that changes in the composition of foundation species (either the addition or removal of macroalgae species) will lead to consequences for the integrity and functioning of ecosystems (Crooks, 2002; Gribben et al., 2013; McKinnon et al., 2009; Ramus et al., 2017). Macroalgal communities (and their associated epifauna) vary between the analyzed sites, which derives from the different conditions present in each of them (different habitat complexities, coastal exposure, depths, etc.) (Contreras-Silva et al., 2020; Horta-Puga et al., 2020; Stagnol et al., 2016; Tribollet et al., 2010). The variation of macroalgae between and within habitat in every site is also shaped by temporal variations at different scales ranging from months to years, and factors such as temperature, abundance of epiphytic algae, productivity, predation pressure, competition, or recruitment (Bertocci et al., 2005; Botwe et al., 2015; Kennelly, 1987; Menconi et al., 1999; Piazzi et al., 2012) contribute to this variation. The marine benthic environment is recognized to be highly variable over different scales of time and space (Horta-Puga et al., 2020). It would be highly important, in future studies, to carry out an integrated analysis of temporal and spatial variability. A continuous long-term analysis of macroalgal assemblages in the Arrábida MPA area, combined with on-going detailed species-level analyses, will allow the detection of trends and oscillations in the macroalgae community (and its epifauna by association). In conclusion, a spatiotemporal analysis would be beneficial to discover important and more detailed information about the dynamics and complexity of relationships between species and their role in ecosystems.

Given the large amount of different habitats and biogeographical diversity, Portugal is one of the countries with the greatest marine biodiversity in the European Union (Delbaere & Consulting, 2002). The rocky reefs of the Arrábida MPA are known to support one of the highest levels of coastal biodiversity in mainland Portugal (Cunha et al., 2014), so studies like this are fundamental to achieve goals that compromise greater conservation, the use of resources in a more sustainable way, and increase financial support for the protection of biodiversity. Continuous support is needed for scientific projects that focus on the difficult and dynamic task that is the assessment of biodiversity, being projects that demonstrate that protecting zones with high ecological value brings great environmental and socio-economic benefits.

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Appendix A

Table A0.1- List of epifaunal taxa found in the community studied, with respective functional group for each trait selected. Based on available literature and online databases. I.O: impossible to obtain - the information available or taxa analyzed are too general to reach the desired level of detail.

Taxa	***Potential size***	***Diet***	***Feeding mode***	***Adult life habit***	***Adult movement***	***Degree of attachment***	***Sociability***	***References****
Achelia spp.	Small (2-5cm)	Microcarnivores	Predator	Interstitial	Crawler	None	Gregarious	[1],[2],[3],[9]
Alpheidae	Small (2-5cm)	Macrocarnivores	Carrion-feeders	Interstitial	Swimmer	None	Gregarious	[1],[2],[3],[9]
Alvania beanii	Very Small (<2cm)	Detritivores/Herbivores	Detritivore/Grazer	Interstitial	Crawler	None	Solitary	[1],[2],[3],[11],[12]
Alvania punctura	Very Small (<2cm)	Detritivores/Herbivores	Detritivore/Grazer	Interstitial	Crawler	None	Solitary	[1],[2],[3],[11],[12]
Alvania spp.	Very Small (<2cm)	Detritivores/Herbivores	Detritivore/Grazer	Interstitial	Crawler	None	Solitary	[1],[2],[3],[9],[11],[12]
Ammotheidae	Small (2-5cm)	Microcarnivores	Predator	Interstitial	Crawler	None	Gregarious	[1],[2],[3],[7],[9]
Amphilochidae	Very Small (<2cm)	Detritivores	Deposit-feeders	Interstitial	Crawler	None	I.O	[1],[2],[3],[4],[6]
Amphilochus manudens	Very Small (<2cm)	Detritivores	Deposit-feeders	Interstitial	Crawler	None	I.O	[1],[2],[3],[4],
Amphilochus spp.	Very Small (<2cm)	Detritivores	Deposit-feeders	Interstitial	Crawler	None	I.O	[1],[2],[3],[4],[6]
Amphipoda	I.O	I.O	I.O	I.O	I.O	I.O	I.O	I.O
Amphipolis spp.	Small–medium (5-10cm)	Omnivores	Suspension/Deposit-feeders	Interstitial	Burrower/Crawler	None	Gregarious	[1],[2],[3],[7],[9]
Amphitholina cuniculus	Very Small (<2cm)	Detritivores/Herbivores	Detritivore/Grazer	Domicolous/Interstitial	Crawler	Temporary	Gregarious	[1],[2],[3],[4]
Amphiuridae	Small–medium (5-10cm)	Omnivores	Suspension/Deposit-feeders	Interstitial	Burrower/Crawler	None	Gregarious	[1],[2],[3],[7],[9]
Ampithoidae	Very Small (<2cm)	Detritivores/Herbivores	Detritivore/Grazer	Domicolous/Interstitial	Crawler	Temporary	Gregarious	[1],[2],[3],[4],
Anthura spp.	Very Small (<2cm)	Microcarnivores	Carrion-feeders	Interstitial	Swimmer	Temporary	Solitary	[1],[2],[3],[9]

Table A1 (continued)

Taxa	*Potential size*	*Diet*	*Feeding mode*	*Adult life habit*	*Adult movement*	*Degree of attachment*	*Sociability*	*References**
Anthuridae	Very Small (<2cm)	Microcarnivores	Carrion-feeders	Interstitial	Swimmer	Temporary	Solitary	[1],[2],[3],[9]
Aora spp.	Very Small (<2cm)	Omnivores	Suspension/Deposit-feeders	Domicolous/Interstitial	Swimmer/Crawler	Temporary	Solitary	[1],[2],[3],[4]
Aoridae	Very Small (<2cm)	Omnivores	Suspension/Deposit-feeders	Domicolous/Interstitial	Swimmer/Crawler	Temporary	Solitary	[1],[2],[3],[4],[6],[7]
Apherusa spp.	Very Small (<2cm)	Detritivores	Deposit-feeders	Interstitial	Swimmer	None	Solitary	[1],[2],[3],[4],[9]
Aplysia spp.	Medium–large (15-30cm)	Herbivores	Grazer	Interstitial	Crawler	None	Solitary/Gregarious	[1],[2],[3]
Aplysiidae	Medium–large (15-30cm)	Herbivores	Grazer	Interstitial	Crawler	None	Solitary/Gregarious	[1],[2],[3],[9],[11],[12]
Apseudes spp.	Very Small (<2cm)	Detritivores	Suspension-feeders	Fossorial	Burrower/Crawler	None	Gregarious	[1],[2],[3],[9]
Apseudidae	Very Small (<2cm)	Detritivores	Suspension-feeders	Fossorial	Burrower/Crawler	None	Gregarious	[1],[2],[3],[9]
Apseudopsis spp.	Very Small (<2cm)	Detritivores	Suspension-feeders	Fossorial	Burrower/Crawler	None	Gregarious	[1],[2],[3],[9]
Arachnida	Very Small (<2cm)	Microcarnivores	Predator	Interstitial	Crawler	None	Gregarious	[1],[2],[3],[9]
Aspidosiphonidae	Medium–large (15-30cm)	Omnivores	Deposit-feeders	Interstitial/Fossorial	Burrower	Temporary	Gregarious	[1],[2],[3],[5]
Astacilla damnoniensis	Very Small (<2cm)	Detritivores	Suspension-feeders	Epi-/endozoic or epi-/endophytic	Crawler	Temporary	Solitary/Gregarious	[1],[2],[3]
Asterinidae	Small (2-5cm)	Omnivores	Carrion-feeders	Interstitial	Crawler	None	Solitary	[1],[2],[3],[7],[9]
Athanas spp.	Small (2-5cm)	Macrocarnivores	Carrion-feeders	Interstitial	Swimmer	None	Gregarious	[1],[2],[3],[9]
Atylidae	Very Small (<2cm)	Herbivores	Grazer	Interstitial	Swimmer	None	Solitary	[1],[2],[3],[4],[6]
Barleeia unifasciata	Very Small (<2cm)	Detritivores/Herbivores	Deposit-feeders/Grazer	Interstitial	Crawler	None	Solitary	[1],[2],[3],[9],[11],[12]

Table A1 (continued)

Taxa	***Potential size***	***Diet***	***Feeding mode***	***Adult life habit***	***Adult movement***	***Degree of attachment***	***Sociability***	***References****
Barleeiidae	Very Small (<2cm)	Detritivores/Herbivores	Deposit-feeders/Grazer	Interstitial	Crawler	None	Solitary	[1],[2],[3],[11],[12]
Bathyporeiidae	Very Small (<2cm)	Detritivores	Deposit-feeders	Fossorial	Burrower/Swimmer	Temporary	Solitary	[1],[2],[3],[9]
Bdellidae	Very Small (<2cm)	Microcarnivores	Predator	Interstitial	Crawler	None	Gregarious	[1],[2],[3],[9]
Bittium reticulatum	Small (2-5cm)	Detritivores/Herbivores	Deposit-feeders/Grazer	Interstitial	Crawler	None	Gregarious	[1],[2],[3],[9],[11],[12]
Blenniidae	Very Large (>50cm)	Omnivores	Predator	Interstitial	Swimmer	None	Solitary/Gregarious	[1],[2],[3]
Calliopiidae	Very Small (<2cm)	Detritivores	Deposit-feeders	Interstitial	Swimmer	None	Solitary	[1],[2],[3],[4],[9]
Callipallene spp.	Small (2-5cm)	Microcarnivores	Parasite	Epi-/endozoic or epi-/endophytic	Crawler	None	Gregarious	[1],[2],[3],[4],[9]
Callipallenidae	Small (2-5cm)	Microcarnivores	Parasite	Epi-/endozoic or epi-/endophytic	Crawler	None	Gregarious	[1],[2],[3],[4],[9]
Capitellidae	Small–medium (5-10cm)	Detritivores	Deposit-feeders	Domicolous/Fossorial	Burrower	Temporary	Gregarious	[1],[2],[3],[7],[9],[10]
Caprella acanthifera	Small (2-5cm)	Herbivores	Carrion-feeders	Interstitial	Swimmer	None	Solitary	[1],[2],[3],[4],[6],[9]
Caprella linearis	Small (2-5cm)	Detritivores	Deposit-feeders	Interstitial	Swimmer	None	Solitary	[1],[2],[3],[4],[6]
Caprella santosrosai	Small (2-5cm)	Omnivores	Deposit-feeders	Interstitial	Swimmer	None	Solitary	[1],[2],[3],[4],[6],[9]
Caprella spp.	Small (2-5cm)	Omnivores	Deposit-feeders	Interstitial	Swimmer	None	Solitary	[1],[2],[3],[4],[6],[9]
Caprellidae	Small (2-5cm)	Omnivores	Deposit-feeders	Interstitial	Swimmer	None	Solitary	[1],[2],[3],[4],[6],[9]
Carcinidae	Small–medium (5-10cm)	Omnivores	Predator	Interstitial	Crawler	None	Solitary	[1],[2],[3]
Cerithiidae	Small (2-5cm)	Detritivores/Herbivores	Deposit-feeders/Grazer	Interstitial	Crawler	None	Gregarious	[1],[2],[3],[11],[12]
Cerithiopsidae	Very Small (<2cm)	Microcarnivores	Predator	Interstitial	Crawler	None	Gregarious	[1],[2],[3],[11],[12]

Table A1 (continued)

Taxa	***Potential size***	***Diet***	***Feeding mode***	***Adult life habit***	***Adult movement***	***Degree of attachment***	***Sociability***	***References****
Cerithiopsis tubercularis	Very Small (<2cm)	Microcarnivores	Predator	Interstitial	Crawler	None	Gregarious	[1],[2],[3],[11],[12]
Chauvetiidae	Small (2-5cm)	Microcarnivores	Predator	Interstitial	Crawler	None	Solitary	[1],[2],[3],[9],[11],[12]
Chondrochelia savignyi	Very Small (<2cm)	Detritivores	Suspension/Deposit-feeders	Domicolous/Fossorial	Burrower/Crawler	Temporary	Gregarious	[1],[2],[3]
Chondrochelia spp.	Very Small (<2cm)	Detritivores	Suspension/Deposit-feeders	Domicolous/Fossorial	Burrower/Crawler	Temporary	Gregarious	[1],[2],[3]
Cingulopsidae	Very Small (<2cm)	Detritivores/Herbivores	Deposit-feeders/Grazer	Interstitial	Crawler	None	Solitary	[1],[2],[3]
Clitellata	Small–medium (5-10cm)	Detritivores	Deposit-feeders	Fossorial	Burrower	Temporary	Solitary	[1],[2],[3],[9],[10]
Corophiidae	Small (2-5cm)	Detritivores	Suspension/Deposit-feeders	Domicolous	Burrower/Crawler	Temporary	Gregarious	[1],[2],[3],[6],[7],[9]
Corophium spp.	Small (2-5cm)	Detritivores	Suspension/Deposit feeders	Domicolous	Burrower/Crawler	Temporary	Gregarious	[1],[2],[3],[6],[7],[9]
Crangonidae	Medium–large (15-30cm)	Macrocarnivores	Predator	Interstitial	Burrower	None	Solitary	[1],[2],[3],[7],[9]
Crisilla spp.	Very Small (<2cm)	Detritivores/Herbivores	Deposit-feeders/Grazer	Interstitial	Crawler	None	Gregarious	[1],[2],[3],[11],[12]
Cumacea	Very Small (<2cm)	Detritivores	Suspension/Deposit-feeders	Fossorial	Burrower/Swimmer	None	Solitary	[1],[2],[3],[7],[9]
Cyrillia spp.	Small–medium (5-10cm)	Microcarnivores	Predator	Interstitial	Crawler	None	Solitary	[1],[2],[3],[11],[12]
Decapoda	I.O	I.O	I.O	I.O	I.O	I.O	I.O	I.O
Dexamine spp.	Small (2-5cm)	Omnivores	Suspension/Deposit-feeders	Interstitial/Fossorial	Burrower/Crawler	None	Solitary	[1],[2],[3],[4],[6],

Table A1 (continued)

Taxa	*Potential size*	*Diet*	*Feeding mode*	*Adult life habit*	*Adult movement*	*Degree of attachment*	*Sociability*	*References**
Dexaminidae	Small (2-5cm)	Omnivores	Suspension/Deposit-feeders	Interstitial/Fossorial	Burrower/Crawler	None	Solitary	[1],[2],[3],[4],[6]
Diastylidae	Small (2-5cm)	Detritivores	Suspension/Deposit-feeders	Fossorial	Burrower/Swimmer	None	Solitary	[1],[2],[3],[9]
Diastylis spp.	Small (2-5cm)	Detritivores	Suspension/Deposit-feeders	Fossorial	Burrower/Swimmer	None	Solitary	[1],[2],[3],[9]
Dynamene spp.	Very Small (<2cm)	Herbivores	Deposit-feeders/Grazer	Interstitial	Burrower/Crawler	None	Gregarious	[1],[2],[3]
Eatonina fulgida	Very Small (<2cm)	Detritivores/Herbivores	Deposit-feeders/Grazer	Interstitial	Crawler	None	Solitary	[1],[2],[3],[11],[12]
Eualus occultus	Small (2-5cm)	Omnivores	Carrion-feeders	Interstitial	Crawler	None	Solitary	[1],[2],[3]
Eualus spp.	Small (2-5cm)	Omnivores	Carrion-feeders	Interstitial	Crawler	None	Solitary	[1],[2],[3],[9]
Eulimidae	Very Small (<2cm)	Macrocarnivores	Parasite	Epi-/endozoic or epi-/endophytic	Crawler	Temporary	Gregarious	[1],[2],[3],[11],[12]
Fibulariidae	Small (2-5cm)	Detritivores	Deposit-feeders	Fossorial	Burrower	None	Solitary	[1],[2],[3],[7]
Gammaridae	Small (2-5cm)	Detritivores	Deposit-feeders	Interstitial/Fossorial	Swimmer/ Crawler/ Burrower	None	Solitary	[1],[2],[3]
Gibbula spp.	Small (2-5cm)	Herbivores	Grazer	Interstitial	Crawler	None	Gregarious	[1],[2],[3],[7],[9],[11],[12]
Gnathia spp.	Very Small (<2cm)	Macrocarnivores	Parasite	Epi-/endozoic or epi-/endophytic	Burrower/Crawler	Temporary	I.O	[1],[2],[3],[9]
Gnathiidae	Very Small (<2cm)	Macrocarnivores	Parasite	Epi-/endozoic or epi-/endophytic	Burrower/Crawler	Temporary	Solitary	[1],[2],[3],[9]
Gobiesocidae	Medium–large (15-30cm)	Omnivores	Predator	Interstitial	Swimmer	None	Solitary	[1],[2],[3]

Table A1 (continued)

Taxa	***Potential size***	***Diet***	***Feeding mode***	***Adult life habit***	***Adult movement***	***Degree of attachment***	***Sociability***	***References****
Heteronemertea	Small (2-5cm)	Macrocarnivores	Predator	Epi-/endozoic or epi-/endophytic	Swimmer/Crawler	Temporary	Gregarious	[1],[2],[3],[5]
Hippolyte spp.	Small–medium (5-10cm)	Macrocarnivores	Carrion-feeders	Interstitial	Swimmer	None	Solitary	[1],[2],[3],[7],[9]
Hippolytidae	Small–medium (5-10cm)	Macrocarnivores	Carrion-feeders	Interstitial	Swimmer	None	Solitary	[1],[2],[3],[7],[9]
Hyalidae	Very Small (<2cm)	Omnivores	Deposit-feeders	Interstitial	Swimmer	None	Gregarious	[1],[2],[3],[4],[9]
Idoteidae	Small (2-5cm)	Omnivores	Carrion-feeders	Interstitial	Crawler	None	Solitary	[1],[2],[3],[9]
Inachidae	Small (2-5cm)	Macrocarnivores	Predator	Interstitial	Crawler	None	Solitary	[1],[2],[3],[9]
Iphimedia spp.	Small (2-5cm)	Omnivores	Carrion-feeders	Epi-/endozoic or epi-/endophytic	Burrower/Swimmer	Temporary	Gregarious	[1],[2],[3],[4],[9]
Iphimediidae	Small (2-5cm)	Omnivores	Carrion-feeders	Epi-/endozoic or epi-/endophytic	Burrower/Swimmer	Temporary	Gregarious	[1],[2],[3],[4],[9]
Isaeidae	Very Small (<2cm)	Detritivores	Suspension/Deposit-feeders	Domicolous	Burrower/Crawler	Temporary	Solitary	[1],[2],[3],[7]
Ischyroceridae	Small (2-5cm)	Detritivores	Suspension-feeders	Domicolous	Burrower	Temporary	Gregarious	[1],[2],[3],[6],
Janiridae	Small (2-5cm)	Herbivores	Deposit-feeders/Grazer	Interstitial	Crawler	None	Solitary	[1],[2],[3],[9]
Jujubinus spp.	Small (2-5cm)	Herbivores	Grazer	Interstitial	Crawler	None	Gregarious	[1],[2],[3],[7],[11],[12]
Leptochelia spp.	Very Small (<2cm)	Detritivores	Suspension/Deposit-feeders	Domicolous/Fossorial	Burrower/Crawler	Temporary	Gregarious	[1],[2],[3],[9]
Leptocheliidae	Very Small (<2cm)	Detritivores	Suspension/Deposit-feeders	Domicolous/Fossorial	Burrower/Crawler	Temporary	Gregarious	[1],[2],[3],[9]

Table A1 (continued)

Taxa	***Potential size***	***Diet***	***Feeding mode***	***Adult life habit***	***Adult movement***	***Degree of attachment***	***Sociability***	***References****
Leucothoe spinicarpa	Small (2-5cm)	Detritivores	Parasite	Epi-/endozoic or epi-/endophytic	Burrower	Temporary	Gregarious	[1],[2],[3],[4],[6],[9]
Leucothoe spp.	Small (2-5cm)	Detritivores	Parasite	Epi-/endozoic or epi-/endophytic	Burrower	Temporary	Gregarious	[1],[2],[3],[4],[6],[9]
Leucothoidae	Small (2-5cm)	Detritivores	Parasite	Epi-/endozoic or epi-/endophytic	Burrower	Temporary	Gregarious	[1],[2],[3],[4],[6],[9]
Lysianassa spp.	Very Small (<2cm)	Omnivores	Carrion-feeders	Interstitial	Swimmer/Crawler	None	Solitary	[1],[2],[3],[4],[6],[9]
Lysianassidae	Very Small (<2cm)	Omnivores	Carrion-feeders	Interstitial	Swimmer/Crawler	None	Solitary	[1],[2],[3],[4],[6],[9]
Maeridae	Very Small (<2cm)	Detritivores	Deposit-feeders	Interstitial	Swimmer/Crawler	None		[1],[2],[3],[4],[9]
Majidae	Medium (10-15cm)	Omnivores	Carrion-feeders	Interstitial	Crawler	None	Solitary	[1],[2],[3],[7]
Mangeliidae	Small (2-5cm)	Microcarnivores	Predator	Interstitial	Crawler	None	Solitary	[1],[2],[3],[11],[12]
Manzonia crassa	Very Small (<2cm)	Detritivores/Herbivores	Deposit-feeders/Grazer	Interstitial	Crawler	None	Solitary	[1],[2],[3],[11],[12]
Manzonia spp.	Very Small (<2cm)	Detritivores/Herbivores	Deposit-feeders/Grazer	Interstitial	Crawler	None	Solitary	[1],[2],[3],[11],[12]
Melitidae	Very Small (<2cm)	Detritivores	Deposit-feeders	Interstitial	Swimmer/Crawler	None	Gregarious	[1],[2],[3],[4],[6],[7],[9]
Munnidae	Very Small (<2cm)	Herbivores	Deposit-feeders/Grazer	Interstitial	Swimmer/Crawler	None	Solitary	[1],[2],[3]
Muricidae	Small–medium (5-10cm)	Microcarnivores	Predator	Interstitial	Crawler	None	Gregarious	[1],[2],[3],[11],[12]
Mysidae	Small (2-5cm)	Omnivores	Suspension feeders	Interstitial	Swimmer/Crawler	None	Gregarious	[1],[2],[3],[7],[9]
Nannastacus spp.	Very Small (<2cm)	Omnivores	Predator	Fossorial	Swimmer/ Crawler/ Burrower	None	Solitary	[1],[2],[3]

Table A1 (continued)

Taxa	*Potential size*	*Diet*	*Feeding mode*	*Adult life habit*	*Adult movement*	*Degree of attachment*	*Sociability*	*References**
Nassariidae	Small (2-5cm)	Microcarnivores	Carrion-feeders	Interstitial	Crawler	None	Gregarious	[1],[2],[3],[7],[9],[11],[12]
Nebaliidae	Very Small (<2cm)	Detritivores/ Microcarnivores	Carrion-feeders	Interstitial	Burrower/Swimmer	None	Gregarious	[1],[2],[3],[9]
Nematoda	Small (2-5cm)	Omnivores	Predator	Epi-/endozoic or epi-/endophytic	Swimmer/Crawler	Temporary	Gregarious	[1],[2],[3],[5]
Nereididae	Medium–large (15-30cm)	Herbivories/ Detritivores/ Omnivores/ Microcarnivores	Deposit-feeders	Interstitial/Fossorial	Swimmer/ Crawler/ Burrower	None	Solitary	[1],[2],[3],[7],[9],[10]
Nototropis swammerdamei	Very Small (<2cm)	Herbivores	Grazer	Interstitial	Swimmer	None	Solitary	[1],[2],[3],[4]
Nudibranchia	Medium–large (15-30cm)	Microcarnivores	Predator	Interstitial	Crawler	None	Solitary	[1],[2],[3],[5],[11],[12]
Obtusella intersecta	Very Small (<2cm)	Detritivores/Herbivores	Deposit-feeders/Grazer	Interstitial	Crawler	None	Solitary	[1],[2],[3],[11],[12]
Ocinebrina aciculata	Small (2-5cm)	Microcarnivores	Predator	Interstitial	Crawler	None	Gregarious	[1],[2],[3],[11],[12]
Odostomia spp.	Very Small (<2cm)	Macrocarnivores	Parasite	Epi-/endozoic or epi-/endophytic	Crawler	Temporary	Gregarious	[1],[2],[3],[9],[11],[12]
Oenonidae	Medium–large (15-30cm)	Microcarnivores	Parasite	Interstitial/Fossorial	Burrower/Crawler	Temporary	Solitary	[1],[2],[3],[9],[10]
Omalogyridae	Very Small (<2cm)	Herbivores	Grazer	Interstitial	Crawler	None	Gregarious	[1],[2],[3],[11],[12]
Ophiothrix spp.	Small–medium (5-10cm)	Detritivores	Suspension-feeders	Interstitial	Crawler	None	Solitary	[1],[2],[3],[7],[9]
Ophiotrichidae	Small–medium (5-10cm)	Detritivores	Suspension-feeders	Interstitial	Crawler	None	Solitary	[1],[2],[3],[7],[9]
Ophiuridae	Small–medium (5-10cm)	Omnivores	Carrion-feeders	Interstitial	Burrower/Crawler	None	Gregarious	[1],[2],[3],[7],[9]

Table A1 (continued)

Taxa	*Potential size*	*Diet*	*Feeding mode*	*Adult life habit*	*Adult movement*	*Degree of attachment*	*Sociability*	*References**
Ophiuroidea	Small (2-5cm)	Herbivories/ Detritivores/ Omnivores/ Microcarnivore	I.O	Interstitial	Crawler	None	Gregarious	[1],[2],[3],[7],[9]
Paranthuridae	Very Small (<2cm)	Microcarnivores	Predator	Interstitial	Crawler	None	I.O	[1],[2],[3]
Paratanaoidea incertae sedis	Very Small (<2cm)	Detritivores	Suspension/Deposit-feeders	Domicolous/Fossorial	Burrower/Crawler	Temporary	Gregarious	[1],[2],[3]
Parechinidae	Medium–large (15-30cm)	Herbivores	Grazer	Interstitial	Crawler	None	Gregarious	[1],[2],[3],[7]
Parthenina spp.	Small (2-5cm)	Macrocarnivores	Parasite	Epi-/endozoic or epi-/endophytic	Crawler	Temporary	Gregarious	[1],[2],[3],,[11],[12]
Pereionotus testudo	Small (2-5cm)	I.O	I.O	Interstitial	Swimmer/Crawler	None	Gregarious	[1],[2],[3]
Philinidae	Small (2-5cm)	Microcarnivores	Predator	Interstitial	Crawler	None	Solitary	[1],[2],[3],[9]
Photidae	Very Small (<2cm)	Omnivores	Suspension/Deposit-feeders	Domicolous	Burrower/Crawler	Temporary	Solitary	[1],[2],[3],[4],[6],[9]
Photis spp.	Very Small (<2cm)	Omnivores	Suspension/Deposit-feeders	Domicolous	Burrower/Crawler	Temporary	Solitary	[1],[2],[3],[4],[6],[9]
Phoxocephalidae	Very Small (<2cm)	Microcarnivores	Predator	Fossorial	Burrower	None	Solitary	[1],[2],[3],[4],[6],[9]
Phtisica marina	Small (2-5cm)	Omnivores	Deposit-feeders	Interstitial	Swimmer	None	Solitary	[1],[2],[3],[4],[6],[9]
Phtisica spp.	Small (2-5cm)	Omnivores	Deposit-feeders	Interstitial	Swimmer	None	Solitary	[1],[2],[3],[4],[6],[9]
Pilumnus hirtellus	Small (2-5cm)	Omnivores	Carrion-feeders	Interstitial	Crawler	None	Solitary	[1],[2],[3],[4],[7],[9]
Pilumnus spp.	Small (2-5cm)	Omnivores	Carrion-feeders	Interstitial	Crawler	None	Solitary	[1],[2],[3],[4],[7],[9]
Pisidia spp.	Small (2-5cm)	Omnivores	Suspension-feeders	Interstitial	Crawler	None	Solitary	[1],[2],[3],[7],[9]
Platyhelminthes	Small (2-5cm)	Macrocarnivores	Predator	Interstitial	Swimmer/Crawler	None	Solitary	[1],[2],[3],[5],[8]

Table A1 (continued)

Taxa	*Potential size*	*Diet*	*Feeding mode*	*Adult life habit*	*Adult movement*	*Degree of attachment*	*Sociability*	*References**
Podoceridae	Very Small (<2cm)	Detritivores	Suspension-feeders	Interstitial	Swimmer/Crawler	None	Gregarious	[1],[2],[3],[4],[9]
Polynoidae	Medium–large (15-30cm)	Microcarnivores	Carrion-feeders	Interstitial	Crawler	Temporary	Gregarious	[1],[2],[3],[7],[9],[10]
Polyplacophora	Small (2-5cm)	Herbivories/ Omnivores	Predator	Interstitial	Crawler	None	Solitary	[1],[2],[3],[5]
Processa spp.	Small (2-5cm)	Microcarnivores	Carrion-feeders	Interstitial	Crawler	None	Solitary	[1],[2],[3],[9]
Pseudoparatanais spp.	Very Small (<2cm)	Detritivores	Suspension/Deposit-feeders	Domicolous/Fossorial	Burrower/Crawler	Temporary	Gregarious	[1],[2],[3]
Pseudoprotella phasma	Small (2-5cm)	Omnivores	Deposit-feeders	Interstitial	Swimmer	None	Solitary	[1],[2],[3],[4],[6],[9]
Pseudoprotella spp.	Small (2-5cm)	Omnivores	Deposit-feeders	Interstitial	Swimmer	None	Solitary	[1],[2],[3],[4],[9]
Pyramidellidae	Small (2-5cm)	Macrocarnivores	Parasite	Epi-/endozoic or epi-/endophytic	Crawler	Temporary	Gregarious	[1],[2],[3],[11],[12]
Raphitoma spp.	Small–medium (5-10cm)	Microcarnivores	Predator	Interstitial	Crawler	None	Solitary	[1],[2],[3],[9],[11],[12]
Raphitomidae	Small–medium (5-10cm)	Microcarnivores	Predator	Interstitial	Crawler	None	Solitary	[1],[2],[3],[9],[11],[12]
Raphitomidae	Small–medium (5-10cm)	Microcarnivores	Predator	Interstitial	Crawler	None	Solitary	[1],[2],[3],[9],[11],[12]
Retusa obtusa	Very Small (<2cm)	Macrocarnivores	Predator	Interstitial	Crawler	None	Solitary	[1],[2],[3],[9],[11],[12]
Retusa spp.	Very Small (<2cm)	Macrocarnivores	Predator	Interstitial	Crawler	None	Solitary	[1],[2],[3],[9],[11],[12]
Retusa truncatula	Very Small (<2cm)	Macrocarnivores	Predator	Interstitial	Crawler	None	Solitary	[1],[2],[3],[9],[11],[12]
Retusidae	Very Small (<2cm)	Macrocarnivores	Predator	Interstitial	Crawler	None	Solitary	[1],[2],[3],[9],[11],[12]
Rissoa guerinii	Very Small (<2cm)	Detritivores/Herbivores	Deposit-feeders/Grazer	Interstitial	Crawler	None	Solitary	[1],[2],[3],[11],[12]

Table A1 (continued)

Taxa	*Potential size*	*Diet*	*Feeding mode*	*Adult life habit*	*Adult movement*	*Degree of attachment*	*Sociability*	*References**
Rissoa lilacina	Very Small (<2cm)	Detritivores/Herbivores	Deposit-feeders/Grazer	Interstitial	Crawler	None	Solitary	[1],[2],[3],[11],[12]
Rissoa parva	Very Small (<2cm)	Detritivores/Herbivores	Deposit-feeders/Grazer	Interstitial	Crawler	None	Solitary	[1],[2],[3],[11],[12]
Rissoa spp.	Very Small (<2cm)	Detritivores/Herbivores	Deposit-feeders/Grazer	Interstitial	Crawler	None	Solitary	[1],[2],[3],[11],[12]
Rissoella spp.	Very Small (<2cm)	Detritivores/Herbivores	Deposit-feeders/Grazer	Interstitial	Crawler	None	Solitary	[1],[2],[3],[11],[12]
Rissoellidae	Very Small (<2cm)	Detritivores/Herbivores	Deposit-feeders/Grazer	Interstitial	Crawler	None	Solitary	[1],[2],[3],[11],[12]
Rissoidae	Small (2-5cm)	Detritivores/Herbivores	Deposit-feeders/Grazer	Interstitial	Crawler	None	Solitary	[1],[2],[3],[11],[12]
Sabellidae	Small–medium (5-10cm)	Detritivores	Suspension-feeders	Domicolous	Sessile	Permanent	Gregarious	[1],[2],[3],[7],[9],[10]
Serpulidae	Small–medium (5-10cm)	Detritivores	Suspension-feeders	Domicolous	Sessile	Permanent	Solitary/Colonial	[1],[2],[3],[7],[9],[10]
Setia spp.	Very Small (<2cm)	Detritivores/Herbivores	Deposit-feeders/Grazer	Interstitial	Crawler	None	Solitary	[1],[2],[3],[11],[12]
Sipuncula	Medium–large (15-30cm)	Detritivores	Deposit-feeders	Fossorial	Burrower	Temporary	Gregarious	[1],[2],[3],[5],[7]
Sphaerodoridae	Small (2-5cm)	Detritivores/ Microcarnivores	Deposit-feeders	Interstitial/Fossorial	Burrower	None	Gregarious	[1],[2],[3],[9],[10]
Sphaeromatidae	Very Small (<2cm)	Herbivores	Deposit-feeders/Grazer	Interstitial	Burrower/Crawler	None	Gregarious	[1][2],[3]
Spiralinella spp.	Small (2-5cm)	Macrocarnivores	Parasite	Epi-/endozoic or epi-/endophytic	Crawler	Temporary	Gregarious	[1],[2],[3],[11],[12]
Stenothoe spp.	Very Small (<2cm)	Microcarnivores	Deposit-feeders	Interstitial	Burrower/Swimmer	None	Solitary	[1],[2],[3],[4],[9]
Stenothoidae	Very Small (<2cm)	Microcarnivores	Deposit-feeders	Interstitial	Burrower/Swimmer	None	Solitary	[1],[2],[3],[4],[9]

Table A1 (continued)

Taxa	*Potential size*	*Diet*	*Feeding mode*	*Adult life habit*	*Adult movement*	*Degree of attachment*	*Sociability*	*References**
Syllidae	Small (2-5cm)	Herbivories/ Detritivores/ Omnivores/ Microcarnivores	Carrion-feeders	Interstitial	Swimmer/ Crawler/ Burrower	None	Solitary	[1],[2],[3],[7],[9],[10]
Tanaidacea	Very Small (<2cm)	Detritivores	Deposit-feeders	Domicolous/Fossorial	Burrower	Temporary	Gregarious	[1],[2],[3],[9]
Tanaididae	Very Small (<2cm)	Detritivores	Deposit-feeders	Domicolous/Fossorial	Burrower	Temporary	Gregarious	[1],[2],[3],[9]
Tanais dulongii	Very Small (<2cm)	Detritivores	Deposit-feeders	Domicolous/Fossorial	Burrower	Temporary	Gregarious	[1],[2],[3],[9]
Tanais spp.	Very Small (<2cm)	Detritivores	Deposit-feeders	Domicolous/Fossorial	Burrower	Temporary	Gregarious	[1],[2],[3],[9]
Tanaopsidae	Very Small (<2cm)	Detritivores	Deposit-feeders	Domicolous/Fossorial	Burrower	Temporary	Gregarious	[1],[2],[3]
Thecostraca	Small (2-5cm)	Detritivores	Suspension-feeders	Interstitial	Sessile	Permanent	Gregarious	[1],[2],[3],[9]
Thoridae	Small (2-5cm)	Omnivores	Carrion-feeders	Interstitial	Crawler	None	Solitary	[1],[2],[3]
Tricolia spp.	Small (2-5cm)	Omnivores	Grazer	Interstitial	Crawler	None	Gregarious	[1],[2],[3],[9],[11],[12]
Triphoridae	Small (2-5cm)	Microcarnivores	Predator	Interstitial	Crawler	None	Gregarious	[1],[2],[3],[11],[12]
Triphosa spp.	Very Small (<2cm)	Detritivores	Carrion-feeders	Interstitial	Swimmer/Crawler	None	Gregarious	[1],[2],[3],[9]
Trochidae	Small (2-5cm)	Herbivores	Grazer	Interstitial	Crawler	None	Gregarious	[1],[2],[3],[7],[9],[11],[12]
Tryphosidae	Very Small (<2cm)	Detritivores	Carrion-feeders	Interstitial	Swimmer/Crawler	None	Gregarious	[1],[2],[3],[9]
Velutinidae	Small (2-5cm)	Macrocarnivores	Predator	Interstitial	Crawler	Temporary	Solitary	[1],[2],[3]
Vitreolina spp.	Very Small (<2cm)	Macrocarnivores	Parasite	Epi-/endozoic or epi-/endophytic	Crawler	Temporary	Gregarious	[1],[2],[3],[11],[12]
Xanthidae	Small–medium (5-10cm)	Omnivores	Deposit-feeders/Grazer	Interstitial	Crawler	None	I.O	[1],[2],[3]

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Table A2- Abundances (N), absolute frequency (FA) and relative frequency (FR) of the invertebrates' taxa collected in association with the four HFS (across all the four sites) in the Arrábida MPA.

Taxa	***Treptacantha usneoides***			***Halopteris scoparia***			***Sphaerococcus coronopifolius***			***Saccorhiza polyschides***			
	N	***FA***	***FR***	***N***	***FA***	***FR***	***N***	***FA***	***FR***	***N***	***FA***	***FR***	***N (TOTAL)***
Phylum Annelida													
Aspidosiphonidae	-	0	0	-	0	0	3	8.33	0.51	-	0	0	3
Capitellidae	-	0	0	2	8.33	0.54	1	8.33	0.51	7	22.22	0.60	10
Clitellata	-	0	0	-	0	0	-	0	0	2	11.11	0.30	2
Nereididae	6	25	1.65	4	25	1.61	1	8.33	0.51	154	77.78	2.11	165
Oenonidae	-	0	0	1	8.33	0.54	-	0	0	-	0	0	1
Polynoidae	-	0	0	-	0	0	-	0	0	1	11.11	0.30	1
Sabellidae	25	66.67	4.40	23	25	1.61	14	41.67	2.56	5	22.22	0.60	67
Serpulidae	4	25	1.65	1	8.33	0.54	-	0	0	11	55.56	1.51	16
Sipuncula	1	8.33	0.55	-	0	0	1	8.33	0.51	3	33.33	0.91	5
Sphaerodoridae	-	0	0	-	0	0	-	0	0	1	11.11	0.30	1
Syllidae	9	50	3.30	21	41.67	2.69	27	50	3.08	44	100	2.72	101
Phylum Arthropoda													
Alpheidae	1	8.33	0.55	-	0	0	-	0	0	7	33.33	0.91	8
Achelia spp.	2	8.33	0.55	10	16.67	1.08	6	33.33	2.05	4	11.11	0.30	22
Ammotheidae	3	25	1.65	67	83.33	5.38	1	8.33	0.51	2	22.22	0.60	73
Amphilochidae	32	58.33	3.85	17	58.33	3.76	155	75	4.62	2	11.11	0.30	206
Amphilochus manudens	20	8.33	0.55	-	0	0	-	0	0	-	0	0	20
Amphilochus spp.	-	0	0	-	0	0	5	16.67	1.03	-	0	0	5
Amphipoda	11	41.67	2.75	87	66.67	4.30	17	50	3.08	9	33.33	0.91	124
Amphitholina cuniculus	3	25	1.65	-	0	0	-	0	0	13	22.22	0.60	16
Ampithoidae	9	25	1.65	10	50	3.23	-	0	0	28	66.67	1.81	47

Table A2 (continued)

Taxa	***Treptacantha usneoides***			***Halopteris scoparia***			***Sphaerococcus coronopifolius***			***Saccorhiza polyschides***			
	N	***FA***	***FR***	***N***	***FA***	***FR***	***N***	***FA***	***FR***	***N***	***FA***	***FR***	***N (TOTAL)***
Anthura spp.	-	0	0	-	0	0	-	0	0	1	11.11	0.30	1
Anthuridae	-	0	0	-	0	0	1	8.33	0.51	1	11.11	0.30	2
Aora spp.	-	0	0	-	0	0	-	0	0	1	11.11	0.30	1
Aoridae	2	8.33	0.55	95	75	4.84	20	50	3.08	61	88.89	2.42	178
Apherusa spp.	-	0	0	-	0	0	-	0	0	1	11.11	0.30	1
Apseudes spp.	-	0	0	-	0	0	1	8.33	0.51	2	11.11	0.30	3
Apseudidae	1	8.33	0.55	-	0	0	-	0	0	12	33.33	0.91	13
Apseudopsis spp.	1	8.33	0.55	-	0	0	-	0	0	24	44.44	1.21	25
Arachnida	-	0	0	-	0	0	1	8.33	0.51	-	0	0	1
Astacilla damnoniensis	-	0	0	1	8.33	0.54	-	0	0	-	0	0	1
Athanas spp.	-	0	0	-	0	0	1	8.33	0.51	7	22.22	0.60	8
Atylidae	4	16.67	1.10	5	25	1.61	1	8.33	0.51	2	11.11	0.30	12
Bathyporeiidae	-	0	0	1	8.33	0.54	-	0	0	2	22.22	0.60	3
Bdellidae	6	25	1.65	9	25	1.61	4	33.33	2.05	-	0	0	19
Calliopiidae	5	33.33	2.20	13	41.67	2.69	5	16.67	1.03	1	11.11	0.30	24
Callipallene spp.	-	0	0	-	0	0	-	0	0	1	11.11	0.30	1
Callipallenidae	1	8.33	0.55	14	66.67	4.30	1	8.33	0.51	5	44.44	1.21	21
Caprella acanthifera	-	0	0	2	8.33	0.54	1	8.33	0.51	2	11.11	0.30	5
Caprella linearis	-	0	0	2	8.33	0.54	-	0	0	-	0	0	2
Caprella santosrosai	-	0	0	-	0	0	2	8.33	0.51	-	0	0	2
Caprella spp.	44	33.33	2.20	2	8.33	0.54	23	41.67	2.56	14	55.56	1.51	83
Caprellidae	34	50	3.30	18	50	3.23	8	33.33	2.05	3	11.11	0.30	63
Carcinidae	1	8.33	0.55	2	8.33	0.54	-	0	0	5	33.33	0.91	8
Chondrochelia savignyi	-	0	0	-	0	0	2	8.33	0.51	-	0	0	2
Chondrochelia spp.	1	8.33	0.55	-	0	0	1	8.33	0.51	2	22.22	0.60	4

Table A2 (continued)

Taxa	***Treptacantha usneoides***			***Halopteris scoparia***			***Sphaerococcus coronopifolius***			***Saccorhiza polyschides***			
	N	***FA***	***FR***	***N***	***FA***	***FR***	***N***	***FA***	***FR***	***N***	***FA***	***FR***	***N (TOTAL)***
Corophiidae	1	8.33	0.55	4	25	1.61	1	8.33	0.51	35	33.33	0.91	41
Corophium spp.	1	8.33	0.55	1	8.33	0.54	-	0	0	-	0	0	2
Crangonidae	1	8.33	0.55	-	0	0	-	0	0	-	0	0	1
Cumacea	1	8.33	0.55	1	8.33	0.54	1	8.33	0.51	2	22.22	0.60	5
Decapoda	-	0	0	1	8.33	0.54	9	16.67	1.03	-	0	0	10
Dexamine spp.	-	0	0	-	0	0	1	8.33	0.51	-	0	0	1
Dexaminidae	7	41.67	2.75	13	41.67	2.69	1	8.33	0.51	1	11.11	0.30	22
Diastylidae	-	0	0	-	0	0	-	0	0	1	11.11	0.30	1
Diastylis spp.	-	0	0	-	0	0	1	8.33	0.51	-	0	0	1
Dynamene spp.	50	58.33	3.85	4	16.67	1.08	13	50	3.08	7	44.44	1.21	74
Eualus occultus	-	0	0	-	0	0	-	0	0	2	11.11	0.30	2
Eualus spp.	-	0	0	1	8.33	0.54	2	16.67	1.03	5	22.22	0.60	8
Gammaridae	2	16.67	1.10	-	0	0	7	8.33	0.51	3	11.11	0.30	12
Gnathia spp.	-	0	0	-	0	0	9	16.67	1.03	-	0	0	9
Gnathiidae	3	16.67	1.10	2	16.67	1.08	3	8.33	0.51	15	66.67	1.81	23
Hippolyte spp.	-	0	0	-	0	0	11	16.67	1.03	-	0	0	11
Hippolytidae	4	25	1.65	3	16.67	1.08	1	8.33	0.51	-	0	0	8
Hyalidae	-	0	0	-	0	0	1	8.33	0.51	-	0	0	1
Idoteidae	-	0	0	2	8.33	0.54	-	0	0	-	0	0	2
Inachidae	-	0	0	1	8.33	0.54	-	0	0	-	0	0	1
Iphimedia spp.	-	0	0	-	0	0	2	8.33	0.51	-	0	0	2
Iphimediidae	1	8.33	0.55	-	0	0	-	0	0	-	0	0	1
Isaeidae	-	0	0	-	0	0	-	0	0	1	11.11	0.30	1
Ischyroceridae	-	0	0	-	0	0	2	8.33	0.51	-	0	0	2
Janiridae	-	0	0	-	0	0	1	8.33	0.51	-	0	0	1
Leptochelia spp.	-	0	0	1	8.33	0.54	-	0	0	-	0	0	1

Table A2 (continued)

Taxa	***Treptacantha usneoides***			***Halopteris scoparia***			***Sphaerococcus coronopifolius***			***Saccorhiza polyschides***			
	N	***FA***	***FR***	***N***	***FA***	***FR***	***N***	***FA***	***FR***	***N***	***FA***	***FR***	***N (TOTAL)***
Leptocheliidae	1	8.33	0.55	2	16.67	1.08	-	0	0	2	11.11	0.30	5
Leucothoe spinicarpa	-	0	0	-	0	0	1	8.33	0.51	-	0	0	1
Leucothoe spp.	-	0	0	-	0	0	6	16.67	1.03	-	0	0	6
Leucothoidae	12	16.67	1.10	-	0	0	-	0	0	-	0	0	12
Lysianassa spp.	-	0	0	-	0	0	-	0	0	4	22.22	0.60	4
Lysianassidae	-	0	0	-	0	0	-	0	0	10	44.44	1.21	10
Maeridae	-	0	0	-	0	0	-	0	0	1	11.11	0.30	1
Majidae	2	16.67	1.10	1	8.33	0.54	1	8.33	0.51	1	11.11	0.30	5
Melitidae	-	0	0	-	0	0	-	0	0	10	55.56	1.51	10
Munnidae	-	0	0	1	8.33	0.54	-	0	0	-	0	0	1
Mysidae	1	8.33	0.55	-	0	0	1	8.33	0.51	5	33.33	0.91	7
Nannastacus spp.	-	0	0	-	0	0	-	0	0	1	11.11	0.30	1
Nebaliidae	-	0	0	-	0	0	-	0	0	1	11.11	0.30	1
Nototropis swammerdamei	-	0	0	-	0	0	3	8.33	0.51	-	0	0	3
Paranthuridae	-	0	0	-	0	0	-	0	0	1	11.11	0.30	1
Paratanaoidea incertae sedis	2	8.33	0.55	1	8.33	0.54	-	0	0	2	11.11	0.30	5
Pereionotus testudo	-	0	0	-	0	0	2	16.67	1.03	37	88.89	2.42	39
Photidae	23	58.33	3.85	28	75	4.84	4	8.33	0.51	46	77.78	2.11	101
Photis spp.	-	0	0	-	0	0	-	0	0	2	22.22	0.60	2
Phoxocephalidae	1	8.33	0.55	-	0	0	1	8.33	0.51	1	11.11	0.30	3
Phtisica marina	-	0	0	2	8.33	0.54	13	25	1.54	-	0	0	15
Phtisica spp.	1	8.33	0.55	5	8.33	0.54	10	25	1.54	-	0	0	16
Pilumnus hirtellus	1	8.33	0.55	-	0	0	-	0	0	7	33.33	0.91	8
Pilumnus spp.	1	8.33	0.55	-	0	0	2	8.33	0.51	7	44.44	1.21	10
Pisidia spp.	-	0	0	-	0	0	2	16.67	1.03	11	11.11	0.30	13

Table A2 (continued)

Taxa	***Treptacantha usneoides***			***Halopteris scoparia***			***Sphaerococcus coronopifolius***			***Saccorhiza polyschides***			
	N	***FA***	***FR***	***N***	***FA***	***FR***	***N***	***FA***	***FR***	***N***	***FA***	***FR***	***N (TOTAL)***
Podoceridae	2	8.33	0.55	1	8.33	0.54	4	8.33	0.51	1	11.11	0.30	8
Processa spp.	-	0	0	-	0	0	-	0	0	1	11.11	0.30	1
Pseudoparatanais spp.	-	0	0	-	0	0	2	8.33	0.51	-	0	0	2
Pseudoprotella phasma	36	41.67	2.75	1	8.33	0.54	10	33.33	2.05	2	11.11	0.30	49
Pseudoprotella spp.	16	25	1.65	-	0	0	1	8.33	0.51	1	11.11	0.30	18
Sphaeromatidae	12	33.33	2.20	3	25	1.61	6	8.33	0.51	2	22.22	0.60	23
Stenothoe spp.	-	0	0	-	0	0	22	8.33	0.51	-	0	0	22
Stenothoidae	37	58.33	3.85	30	75	4.84	27	41.67	2.56	18	55.56	1.51	112
Tanaidacea	-	0	0	-	0	0	-	0	0	19	11.11	0.30	19
Tanaididae	-	0	0	30	41.67	2.69	1	8.33	0.51	37	22.22	0.60	68
Tanais dulongii	-	0	0	-	0	0	-	0	0	24	33.33	0.91	24
Tanais spp.	-	0	0	6	16.67	1.08	1	8.33	0.51	27	33.33	0.91	34
Tanaopsidae	-	0	0	-	0	0	1	8.33	0.51	-	0	0	1
Thecostraca	3	25	1.65	-	0	0	-	0	0	1	11.11	0.30	4
Thoridae	-	0	0	-	0	0	8	8.33	0.51	2	11.11	0.30	10
Triphosa spp.	-	0	0	-	0	0	-	0	0	1	11.11	0.30	1
Tryphosidae	-	0	0	-	0	0	-	0	0	1	11.11	0.30	1
Xanthidae	-	0	0	-	0	0	-	0	0	3	22.22	0.60	3
Chordata													
Blenniidae	-	0	0	-	0	0	-	0	0	1	11.11	0.30	1
Gobiesocidae	1	8.33	0.55	-	0	0	3	25	1.54	3	33.33	0.91	7
Echinodermata													
Amphiuridae	3	16.67	1.10	4	25	1.61	10	25	1.54	29	88.89	2.42	46

Table A2 (continued)

Taxa	*Treptacantha usneoides*			*Halopteris scoparia*			*Sphaerococcus coronopifolius*			*Saccorhiza polyschides*			
	N	***FA***	***FR***	***N***	***FA***	***FR***	***N***	***FA***	***FR***	***N***	***FA***	***FR***	***N (TOTAL)***
Amphipolis spp.	-	0	0	-	0	0	-	0	0	4	11.11	0.30	4
Asterinidae	1	8.33	0.55	-	0	0	-	0	0	-	0	0	1
Ophiothrix spp.	-	0	0	-	0	0	10	16.67	1.03	-	0	0	10
Ophiotrichidae	2	16.67	1.10	-	0	0	4	8.33	0.51	34	66.67	1.81	40
Ophiuridae	-	0	0	-	0	0	-	0	0	6	22.22	0.60	6
Ophiuroidea	-	0	0	-	0	0	-	0	0	1	11.11	0.30	1
Parechinidae	-	0	0	-	0	0	-	0	0	5	22.22	0.60	5
Fibulariidae	-	0	0	-	0	0	-	0	0	5	22.22	0.60	5
Mollusca													
Aplysia spp.	-	0	0	-	0	0	4	16.67	1.03	-	0	0	4
Alvania beanii	-	0	0	-	0	0	-	0	0	3	11.11	0.30	3
Alvania punctura	-	0	0	-	0	0	-	0	0	17	33.33	0.91	17
Alvania spp.	-	0	0	1	8.33	0.54	-	0	0	3	11.11	0.30	4
Aplysiidae	8	25	1.65	1	8.33	0.54	1	8.33	0.51	-	0	0	10
Barleeia unifasciata	-	0	0	-	0	0	-	0	0	1	11.11	0.30	1
Barleeiidae	2	16.67	1.10	17	16.67	1.08	-	0	0	8	22.22	0.60	27
Bittium reticulatum	1	8.33	0.55	-	0	0	3	25	1.54	77	55.56	1.51	81
Cerithiidae	-	0	0	-	0	0	-	0	0	144	44.44	1.21	144
Cerithiopsidae	-	0	0	-	0	0	-	0	0	5	22.22	0.60	5
Cerithiopsis tubercularis	-	0	0	-	0	0	-	0	0	3	22.22	0.60	3
Chauvetiidae	1	8.33	0.55	-	0	0	-	0	0	-	0	0	1
Cingulopsidae	1	8.33	0.55	30	33.33	2.15	3	8.33	0.51	8	33.33	0.91	42
Crisilla spp.	-	0	0	-	0	0	23	25	1.54	62	22.22	0.60	85
Cyrillia spp.	-	0	0	-	0	0	-	0	0	2	11.11	0.30	2
Eatonina fulgida	1	8.33	0.55	-	0	0	7	25	1.54	7	33.33	0.91	15

Table A2 (continued)

Taxa	*Treptacantha usneoides*			*Halopteris scoparia*			*Sphaerococcus coronopifolius*			*Saccorhiza polyschides*			
	N	***FA***	***FR***	***N***	***FA***	***FR***	***N***	***FA***	***FR***	***N***	***FA***	***FR***	***N (TOTAL)***
Eulimidae	-	0	0	-	0	0	-	0	0	2	11.11	0.30	2
Gibbula spp.	-	0	0	-	0	0	1	8.33	0.51	13	33.33	0.91	14
Jujubinus spp.	-	0	0	-	0	0	-	0	0	8	22.22	0.60	8
Mangeliidae	-	0	0	-	0	0	-	0	0	2	22.22	0.60	2
Manzonia crassa	-	0	0	-	0	0	-	0	0	7	44.44	1.21	7
Manzonia spp.	-	0	0	-	0	0	-	0	0	38	44.44	1.21	38
Muricidae	-	0	0	-	0	0	-	0	0	10	44.44	1.21	10
Nassariidae	-	0	0	-	0	0	-	0	0	9	33.33	0.91	9
Nudibranchia	-	0	0	1	8.33	0.54	5	25	1.54	-	0	0	6
Obtusella intersecta	-	0	0	-	0	0	-	0	0	2	11.11	0.30	2
Ocinebrina aciculata	-	0	0	-	0	0	-	0	0	1	11.11	0.30	1
Odostomia spp.	-	0	0	-	0	0	1	8.33	0.51	2	22.22	0.60	3
Omalogyridae	-	0	0	1	8.33	0.54	-	0	0	7	33.33	0.91	8
Parthenina spp.	-	0	0	-	0	0	-	0	0	2	11.11	0.30	2
Philinidae	-	0	0	-	0	0	2	8.33	0.51	-	0	0	2
Polyplacophora	-	0	0	-	0	0	-	0	0	1	11.11	0.30	1
Pyramidellidae	-	0	0	2	16.67	1.08	-	0	0	11	55.56	1.51	13
Raphitoma spp.	1	8.33	0.55	-	0	0	2	8.33	0.51	3	11.11	0.30	6
Raphitomidae	-	0	0	-	0	0	-	0	0	2	22.22	0.60	2
Raphitomidae	-	0	0	-	0	0	-	0	0	1	11.11	0.30	1
Retusa obtusa	-	0	0	-	0	0	-	0	0	1	11.11	0.30	1
Retusa spp.	-	0	0	-	0	0	-	0	0	4	22.22	0.60	4
Retusa truncatula	-	0	0	-	0	0	-	0	0	1	11.11	0.30	1
Retusidae	-	0	0	-	0	0	-	0	0	2	22.22	0.60	2
Rissoa guerinii	1	8.33	0.55	1	8.33	0.54	11	41.67	2.56	-	0	0	13
Rissoa lilacina	3	25	1.65	-	0	0	5	16.67	1.03	-	0	0	8
Rissoa parva	1	8.33	0.55	-	0	0	-	0	0	-	0	0	1

Table A2 (continued)

Taxa	***Treptacantha usneoides***			***Halopteris scoparia***			***Sphaerococcus coronopifolius***			***Saccorhiza polyschides***			
	N	***FA***	***FR***	***N***	***FA***	***FR***	***N***	***FA***	***FR***	***N***	***FA***	***FR***	***N (TOTAL)***
Rissoa spp.	-	0	0	-	0	0	-	0	0	1	11.11	0.30	1
Rissoella spp.	-	0	0	-	0	0	8	16.67	1.03	1	11.11	0.30	9
Rissoellidae	1	8.33	0.55	2	8.33	0.54	-	0	0	2	11.11	0.30	5
Rissoidae	53	83.33	5.49	46	100	6.45	60	75	4.62	282	88.89	2.42	441
Setia spp.	-	0	0	-	0	0	3	8.33	0.51	-	0	0	3
Spiralinella spp.	-	0	0	-	0	0	-	0	0	1	11.11	0.30	1
Tricolia spp.	7	16.67	1.10	3	25	1.61	9	41.67	2.56	5	33.33	0.91	24
Triphoridae	3	16.67	1.10	-	0	0	18	25	1.54	11	33.33	0.91	32
Trochidae	-	0	0	1	8.33	0.54	1	8.33	0.51	60	88.89	2.42	62
Velutinidae	-	0	0	-	0	0	-	0	0	1	11.11	0.30	1
Vitreolina spp.	-	0	0	-	0	0	-	0	0	4	33.33	0.91	4
Nematoda													
Nematoda	74	66.67	4.40	51	58.33	3.76	23	58.33	3.59	83	100	2.72	231
Nemertea													
Heteronemertea	1	8.33	0.55	1	8.33	0.54	-	0	0	2	22.22	0.60	4
Platyhelminthes													
Platyhelminthes	2	16.67	1.10	-	0	0	-	0	0	-	0	0	2
N (Total)	616			714			715			1811			3856

Table A3- Post hoc pairwise comparisons (from PERMANOVA) of taxonomic composition and functional trait proportions between HFS groups. Bold indicates significant differences. P(MC) < 0.05. P(MC) = probability associated with the Monte Carlo randomization procedure.

HFS Groups	***Taxonomic composition***			
	t	***P(perm)***	***Unique perms***	***P(MC)***
T. usneoides, H. scoparia	1.6113	0.0819	425	**0.0283**
T. usneoides, S. coronopifolius	1.112	0.3141	425	0.3083
T. usneoides, S. polyschides	1.7706	0.0918	212	**0.0205**
H. scoparia, S. coronopifolius	1.4212	0.1114	425	0.0703
H. scoparia, S. polyschides	1.5679	0.173	212	0.0663
S. coronopifolius, S. polyschides	1.5263	0.176	212	0.0607
HFS Groups	***Functional trait proportions***			
	t	***P(perm)***	***Unique perms***	***P(MC)***
T. usneoides, H. scoparia	1.2394	0.2785	425	0.216
T. usneoides, S. coronopifolius	1.7354	0.0997	425	**0.041**
T. usneoides, S. polyschides	1.4039	0.2483	212	0.1479
H. scoparia, S. coronopifolius	1.8729	0.0809	425	**0.0271**
H. scoparia, S. polyschides	1.5371	0.1892	212	0.1064
S. coronopifolius, S. polyschides	1.7185	0.1722	212	0.0618

Table A4- Results of SIMPER taxonomic analysis indicating species contributions to average similarity among sampling HFS.

Taxa	*Average abundance*	*Average contribution to overall similarity (%)*	*Cumulative contribution of the taxa (%)*
		Group *Treptacantha usneoides*	
		% Average similarity: 28.63	
Rissoidae	1.19	4.66	16.26
Nematoda	1.05	3.12	27.17
Amphilochidae	0.8	2.57	36.16
Sabellidae	0.84	2.55	45.06
Dynamene spp.	0.89	1.97	51.94
		Group *Halopteris scoparia*	
		% Average similarity: 37.31	
Rissoidae	1.27	5.8	15.54
Ammotheidae	1.2	4.14	26.62
Aoridae	1.22	3.49	35.97
Stenothoidae	0.95	2.99	43.98
Photidae	0.9	2.83	51.57
		Group *Sphaerococcus coronopifolius*	
		% Average similarity: 22.53	
Amphilochidae	1.22	3.63	16.11
Rissoidae	1.07	3.5	31.64
Nematoda	0.72	1.52	38.39
Syllidae	0.69	1.36	44.42
Aoridae	0.64	1.26	50.03
		Group *Saccorhiza polyschides*	
		%Average similarity: 35.81	
Rissoidae	2	3.09	8.63
Nematoda	1.64	2.96	16.91
Syllidae	1.37	2.45	23.75
Aoridae	1.41	2.27	30.09
Amphiuridae	1.2	2.03	35.77
Trochidae	1.32	1.97	41.26
Pereionotus testudo	1.25	1.9	46.56
Nereididae	1.36	1.55	50.9

Table A5- Results of SIMPER taxonomic analysis to identify taxa contributing most to assemblage differences between HFS, with a 50% cumulative contribution cut-off.

Taxa	***Average abundance***	***Average abundance***	***Average contribution to overall dissimilarity (%)***	***Cumulative contribution of the taxa (%)***
	Treptacantha usneoides	***Halopteris scoparia***		
Aoridae	0.1	1.22	3.12	4.37
Ammotheidae	0.25	1.2	2.88	8.4
Nematoda	1.05	0.93	2.5	11.89
Amphipoda	0.5	1.07	2.45	15.31
Sabellidae	0.84	0.38	2.25	18.46
Dynamene spp.	0.89	0.19	2.19	21.53
Stenothoidae	0.77	0.95	2.11	24.47
Amphilochidae	0.8	0.71	2.08	27.39
Caprellidae	0.69	0.64	2.08	30.29
Photidae	0.78	0.9	2	33.09
Callipallenidae	0.08	0.74	1.91	35.76
Syllidae	0.53	0.58	1.83	38.32
Tanaididae	0	0.64	1.64	40.61
Ampithoidae	0.3	0.55	1.6	42.84
Calliopiidae	0.35	0.52	1.6	45.07
Dexaminidae	0.45	0.5	1.57	47.27
Sphaeromatidae	0.43	0.25	1.55	49.43
Pseudoprotella phasma	0.58	0.08	1.51	51.54
	Treptacantha usneoides	***Sphaerococcus coronopifolius***		
Amphilochidae	0.8	1.22	2.58	3.39
Nematoda	1.05	0.72	2.35	6.49
Stenothoidae	0.77	0.63	2.22	9.4
Dynamene spp.	0.89	0.59	2.15	12.23
Rissoidae	1.19	1.07	2.07	14.95
Sabellidae	0.84	0.52	2	17.58
Caprellidae	0.69	0.39	1.93	20.12
Photidae	0.78	0.12	1.9	22.61
Syllidae	0.53	0.69	1.87	25.08
Caprella spp.	0.51	0.56	1.86	27.53
Pseudoprotella phasma	0.58	0.39	1.77	29.85
Amphipoda	0.5	0.61	1.74	32.14
Aoridae	0.1	0.64	1.74	34.43
Sphaeromatidae	0.43	0.13	1.51	36.42
Tricolia spp.	0.23	0.47	1.47	38.34
Amphiuridae	0.18	0.32	1.25	39.99

Table A5 (continued)

Taxa	*Average abundance*	*Average abundance*	*Average contribution to overall dissimilarity (%)*	*Cumulative contribution of the taxa (%)*
Bdellidae	0.29	0.33	1.21	41.59
Dexaminidae	0.45	0.08	1.17	43.12
Triphoridae	0.18	0.38	1.17	44.66
Rissoa guerinii	0.08	0.48	1.17	46.19
Calliopiidae	0.35	0.21	1.15	47.7
Pseudoprotella spp.	0.36	0.08	1.11	49.17
Phtisica spp.	0.08	0.32	1.01	50.5
	Halopteris scoparia	***Sphaerococcus coronopifolius***		
Ammotheidae	1.2	0.08	2.96	3.88
Aoridae	1.22	0.64	2.45	7.09
Amphilochidae	0.71	1.22	2.45	10.3
Amphipoda	1.07	0.61	2.31	13.34
Nematoda	0.93	0.72	2.26	16.29
Photidae	0.9	0.12	2.25	19.24
Stenothoidae	0.95	0.63	2.13	22.03
Syllidae	0.58	0.69	1.94	24.57
Callipallenidae	0.74	0.08	1.8	26.93
Sabellidae	0.38	0.52	1.75	29.22
Caprellidae	0.64	0.39	1.71	31.46
Tanaididae	0.64	0.08	1.61	33.58
Rissoidae	1.27	1.07	1.61	35.69
Dynamene spp.	0.19	0.59	1.48	37.62
Calliopiidae	0.52	0.21	1.45	39.52
Ampithoidae	0.55	0	1.43	41.4
Caprella spp.	0.1	0.56	1.43	43.27
Cingulopsidae	0.49	0.11	1.36	45.05
Dexaminidae	0.5	0.08	1.28	46.73
Tricolia spp.	0.25	0.47	1.27	48.39
Bdellidae	0.32	0.33	1.25	50.03
	Treptacantha usneoides	***Saccorhiza polyschides***		
Aoridae	0.1	1.41	2.11	2.6
Trochidae	0	1.32	2.04	5.11
Nereididae	0.29	1.36	1.84	7.38
Pereionotus testudo	0	1.25	1.82	9.63
Rissoidae	1.19	2	1.76	11.8
Amphiuridae	0.18	1.2	1.64	13.82
Cerithiidae	0	1.08	1.59	15.79
Bittium reticulatum	0.08	1.01	1.55	17.7

Table A5 (continued)

Taxa	*Average abundance*	*Average abundance*	*Average contribution to overall dissimilarity (%)*	*Cumulative contribution of the taxa (%)*
Ophiotrichidae	0.17	0.95	1.42	19.46
Syllidae	0.53	1.37	1.36	21.14
Nematoda	1.05	1.64	1.33	22.78
Ampithoidae	0.3	0.88	1.27	24.35
Amphilochidae	0.8	0.13	1.26	25.91
Photidae	0.78	1.11	1.24	27.43
Dynamene spp.	0.89	0.5	1.22	28.94
Sabellidae	0.84	0.27	1.19	30.41
Stenothoidae	0.77	0.7	1.14	31.82
Caprella spp.	0.51	0.7	1.14	33.23
Gnathiidae	0.18	0.82	1.11	34.59
Apseudopsis spp.	0.08	0.68	1.06	35.9
Caprellidae	0.69	0.15	1.06	37.21
Manzonia spp.	0	0.7	1.04	38.49
Pyramidellidae	0	0.66	1.01	39.74
Tanais spp.	0	0.58	1	40.97
Serpulidae	0.27	0.65	0.95	42.13
Amphipoda	0.5	0.4	0.92	43.27
Melitidae	0	0.64	0.91	44.39
Pseudoprotella phasma	0.58	0.13	0.88	45.47
Corophiidae	0.08	0.55	0.83	46.49
Sphaeromatidae	0.43	0.22	0.81	47.49
Gnathiidae	0	0.5	0.8	48.48
Pilumnus spp.	0.08	0.5	0.79	49.45
Alvania punctura	0	0.49	0.79	50.42
	Halopteris scoparia	***Saccorhiza polyschides***		
Trochidae	0.08	1.32	1.89	2.44
Pereionotus testudo	0	1.25	1.78	4.75
Nereididae	0.27	1.36	1.78	7.06
Ammotheidae	1.2	0.22	1.61	9.13
Rissoidae	1.27	2	1.57	11.17
Cerithiidae	0	1.08	1.56	13.18
Amphiuridae	0.27	1.2	1.53	15.16
Bittium reticulatum	0	1.01	1.52	17.14
Ophiotrichidae	0	0.95	1.5	19.07
Amphipoda	1.07	0.4	1.43	20.92
Syllidae	0.58	1.37	1.4	22.73
Nematoda	0.93	1.64	1.32	24.44
Aoridae	1.22	1.41	1.21	26

Table A5 (continued)

Taxa	*Average abundance*	*Average abundance*	*Average contribution to overall dissimilarity (%)*	*Cumulative contribution of the taxa (%)*
Tanaididae	0.64	0.46	1.2	27.55
Ampithoidae	0.55	0.88	1.08	28.95
Gnathiidae	0.17	0.82	1.08	30.34
Stenothoidae	0.95	0.7	1.07	31.73
Photidae	0.9	1.11	1.06	33.1
Tanais spp.	0.22	0.58	1.05	34.46
Apseudopsis spp.	0	0.68	1.03	35.78
Manzonia spp.	0	0.7	1.02	37.1
Amphilochidae	0.71	0.13	1.02	38.42
Caprella spp.	0.1	0.7	0.98	39.69
Cingulopsidae	0.49	0.41	0.97	40.95
Caprellidae	0.64	0.15	0.97	42.2
Pyramidellidae	0.17	0.66	0.96	43.44
Serpulidae	0.08	0.65	0.92	44.63
Corophiidae	0.27	0.55	0.91	45.81
Callipallenidae	0.74	0.47	0.9	46.98
Melitidae	0	0.64	0.89	48.12
Calliopiidae	0.52	0.11	0.8	49.16
Gnathiidae	0	0.5	0.78	50.17
	Sphaerococcus coronopifolius	***Saccorhiza polyschides***		
Nereididae	0.08	1.36	1.91	2.32
Trochidae	0.08	1.32	1.87	4.58
Rissoidae	1.07	2	1.81	6.77
Amphilochidae	1.22	0.13	1.74	8.88
Pereionotus testudo	0.17	1.25	1.61	10.84
Photidae	0.12	1.11	1.59	12.76
Cerithiidae	0	1.08	1.55	14.64
Nematoda	0.72	1.64	1.51	16.48
Amphiuridae	0.32	1.2	1.46	18.25
Bittium reticulatum	0.25	1.01	1.46	20.02
Aoridae	0.64	1.41	1.46	21.79
Ophiotrichidae	0.12	0.95	1.45	23.55
Ampithoidae	0	0.88	1.33	25.17
Syllidae	0.69	1.37	1.28	26.72
Stenothoidae	0.63	0.7	1.16	28.12
Gnathiidae	0.11	0.82	1.11	29.46
Caprella spp.	0.56	0.7	1.06	30.75
Apseudopsis spp.	0	0.68	1.02	31.99
Manzonia spp.	0	0.7	1.01	33.22

Table A5 (continued)

Taxa	*Average abundance*	*Average abundance*	*Average contribution to overall dissimilarity (%)*	*Cumulative contribution of the taxa (%)*
Crisilla spp.	0.4	0.49	1	34.44
Tanais spp.	0.08	0.58	0.99	35.64
Pyramidellidae	0	0.66	0.98	36.82
Amphipoda	0.61	0.4	0.95	37.97
Serpulidae	0	0.65	0.92	39.1
Dynamene spp.	0.59	0.5	0.91	40.2
Sabellidae	0.52	0.27	0.89	41.27
Melitidae	0	0.64	0.88	42.34
Triphoridae	0.38	0.46	0.88	43.41
Tricolia spp.	0.47	0.38	0.82	44.4
Eatonina fulgida	0.31	0.39	0.81	45.38
Corophiidae	0.08	0.55	0.81	46.37
Pilumnus spp.	0.1	0.5	0.78	47.31
Gnathiidae	0	0.5	0.77	48.25
Alvania punctura	0	0.49	0.76	49.17
Tanaididae	0.08	0.46	0.75	50.08

Table A6- Results of SIMPER functional analysis indicating traits contributions to average squared distance among sampling HFS.

Traits categories	***Average value***	***Average squared distance***	***Cumulative contribution of the trait categories (%)***
		Group *Treptacantha usneoides*	
		Average squared distance: 0.43	
Domicolous/Fossorial	0.002910	0.000028	0.01
Medium (10-15cm)	0.005680	0.000222	0.06
Fossorial	0.009040	0.000350	0.14
Solitary/Gregarious	0.013000	0.000706	0.3
Interstitial/Fossorial	0.029700	0.000750	0.48
Domicolous/Interstitial	0.020700	0.000873	0.68
Solitary/Colonial	0.015500	0.000959	0.9
Swimmer/Crawler/ Burrower	0.032800	0.001280	1.2
Burrower	0.013900	0.001700	1.59
Parasite	0.018800	0.001720	1.99
Macrocarnivores	0.033700	0.002260	2.51
Carrion-feeders	0.053500	0.002740	3.15
Suspension/Deposit-feeders	0.069600	0.003160	3.88
Permanent	0.069800	0.004180	4.85
Suspension-feeders	0.082900	0.004400	5.86
Herbivores	0.124000	0.004490	6.9
Domicolous	0.099600	0.004600	7.97
Grazer	0.041300	0.004650	9.04
Microcarnivores	0.075000	0.005720	10.37
Burrower/Swimmer	0.052800	0.006170	11.8
Burrower/Crawler	0.177000	0.008830	13.84
Small–medium (5-10cm)	0.102000	0.008970	15.92
Predator	0.151000	0.013600	19.07
Crawler	0.323000	0.014000	22.31
Swimmer/Crawler	0.127000	0.015000	25.78
Epi-/endozoic or epi-/endophytic	0.141000	0.015200	29.29
Detritivore/Grazer	0.255000	0.016500	33.11
Temporary	0.199000	0.017900	37.26
Swimmer	0.176000	0.018300	41.5
Very Small (<2cm)	0.358000	0.019200	45.96
Detritivores	0.205000	0.024200	51.55
		Group *Halopteris scoparia*	
		Average squared distance: 0.43	
Solitary/Colonial	0.001700	0.000035	0.01
Solitary/Gregarious	0.002810	0.000043	0.02
Fossorial	0.004640	0.000119	0.05

Table A6 (continued)

Traits categories	*Average value*	*Average squared distance*	*Cumulative contribution of the trait categories (%)*
Medium (10-15cm)	0.003970	0.000189	0.09
Grazer	0.015900	0.000714	0.26
Macrocarnivores	0.022300	0.000858	0.46
Herbivores	0.031800	0.001170	0.73
Burrower/Swimmer	0.042300	0.001700	1.13
Interstitial/Fossorial	0.030700	0.001720	1.53
Swimmer/Crawler/Burrower	0.040300	0.001790	1.95
Domicolous/Fossorial	0.052500	0.001890	2.39
Parasite	0.036900	0.001920	2.84
Carrion-feeders	0.045900	0.002020	3.32
Burrower	0.046000	0.002090	3.8
Burrower/Crawler	0.091800	0.004020	4.74
Swimmer	0.095500	0.005230	5.96
Permanent	0.036700	0.007270	7.66
Detritivore/Grazer	0.146000	0.007770	9.48
Domicolous	0.077200	0.007850	11.31
Suspension-feeders	0.039200	0.007940	13.17
Deposit-feeders	0.198000	0.009250	15.33
Small–medium (5-10cm)	0.058000	0.009320	17.51
Detritivores	0.146000	0.009820	19.8
Epi-/endozoic or epi-/endophytic	0.130000	0.010700	22.32
Domicolous/Interstitial	0.117000	0.014400	25.67
Omnivores	0.328000	0.014800	29.14
Crawler	0.358000	0.014900	32.63
Interstitial	0.495000	0.015300	36.2
Microcarnivores	0.209000	0.015900	39.92
Suspension/Deposit-feeders	0.175000	0.017500	44
Swimmer/Crawler	0.197000	0.018600	48.34
Solitary	0.476000	0.019700	52.95
		Group *Sphaerococcus coronopifolius* Average squared distance: 0.42	
Medium (10-15cm)	0.003090	0.000114	0.03
Solitary/Gregarious	0.008690	0.000266	0.09
Fossorial	0.012600	0.000503	0.21
Domicolous/Interstitial	0.028800	0.001060	0.46
Permanent	0.025200	0.001490	0.82
Grazer	0.032900	0.001560	1.19
Swimmer/Crawler	0.061600	0.001590	1.57
Domicolous/Fossorial	0.023000	0.001640	1.96
Parasite	0.030300	0.001770	2.39

Table A6 (continued)

Traits categories	*Average value*	*Average squared distance*	*Cumulative contribution of the trait categories (%)*
Macrocarnivores	0.034200	0.002210	2.91
Swimmer/Crawler/ Burrower	0.046500	0.002300	3.46
Domicolous	0.035600	0.002450	4.05
Epi-/endozoic or epi-/endophytic	0.056300	0.002710	4.69
Herbivores	0.054300	0.003470	5.52
Suspension-feeders	0.061200	0.003590	6.38
Predator	0.097500	0.004450	7.44
Interstitial/Fossorial	0.034400	0.004610	8.54
Carrion-feeders	0.068200	0.005400	9.83
Microcarnivores	0.137000	0.006210	11.31
Burrower	0.047500	0.006810	12.94
Suspension/Deposit-feeders	0.089600	0.007060	14.62
Burrower/Swimmer	0.073500	0.007660	16.45
Swimmer	0.152000	0.008040	18.37
Detritivore/Grazer	0.217000	0.008060	20.29
Burrower/Crawler	0.107000	0.008900	22.42
Small–medium (5-10cm)	0.093100	0.010100	24.82
Omnivores	0.269000	0.011400	27.55
Interstitial	0.774000	0.017400	31.7
Temporary	0.136000	0.017900	35.98
None	0.804000	0.018000	40.28
Small (2-5cm)	0.393000	0.020400	45.16
Detritivores	0.250000	0.025700	51.3
		Group *Saccorhiza polyschides* **Average squared distance: 0.36**	
Herbivories/Omnivores	0.000383	0.000001	0
Very Large (>50cm)	0.000450	0.000002	0
Solitary/Gregarious	0.000450	0.000002	0
Medium (10-15cm)	0.000481	0.000002	0
Detritivores/Microcarnivores	0.001380	0.000009	0
Solitary/Colonial	0.005530	0.000053	0.02
Permanent	0.008950	0.000065	0.04
Parasite	0.022700	0.000076	0.06
Swimmer	0.024900	0.000144	0.1
Burrower/Swimmer	0.012500	0.000195	0.15
Macrocarnivores	0.031300	0.000264	0.22
Fossorial	0.032400	0.000587	0.39
Burrower	0.069600	0.000599	0.55
Suspension-feeders	0.059200	0.000718	0.75
Small–medium (5-10cm)	0.068500	0.000848	0.98

Table A6 (continued)

Traits categories	*Average value*	*Average squared distance*	*Cumulative contribution of the trait categories (%)*
Herbivores	0.059200	0.000999	1.26
Grazer	0.054000	0.001060	1.55
Domicolous/Fossorial	0.067900	0.001180	1.87
Carrion-feeders	0.071400	0.001270	2.22
Microcarnivores	0.049400	0.001480	2.63
Detritivores	0.155000	0.001560	3.06
Domicolous/Interstitial	0.063300	0.002480	3.74
Epi-/endozoic or epi-/endophytic	0.083000	0.002990	4.57
Domicolous	0.053800	0.004500	5.81
Burrower/Crawler	0.109000	0.005530	7.33
Predator	0.099100	0.006170	9.03
Swimmer/Crawler	0.140000	0.006430	10.8
Suspension/Deposit-feeders	0.114000	0.007390	12.84
Very Small (<2cm)	0.337000	0.011400	15.99
None	0.724000	0.012700	19.51
Temporary	0.261000	0.013900	23.33
Omnivores	0.205000	0.014200	27.23
Small (2-5cm)	0.504000	0.015200	31.43
Detritivore/Grazer	0.376000	0.027500	39.01
Gregarious	0.509000	0.027700	46.65
Solitary	0.476000	0.029300	54.72

Table A7- Results of SIMPER functional analysis to identify trait contributing most to assemblage differences between HFS, with a 50% cumulative contribution cut-of.

Trait categories	***Average value***	***Average value***	***Average squared distance***	***Cumulative contribution of the trait categories (%)***
	Treptacantha usneoides	***Halopteris scoparia***		
Small (2-5cm)	0.488	0.445	0.0710	7.28
Interstitial	0.67	0.495	0.0697	14.43
None	0.704	0.549	0.0667	21.27
Gregarious	0.385	0.402	0.0621	27.64
Predator	0.151	0.251	0.0544	33.22
Deposit-feeders	0.3	0.198	0.0535	38.7
Temporary	0.199	0.322	0.0531	44.15
Solitary	0.472	0.476	0.0509	49.38
Very Small (<2cm)	0.358	0.387	0.0494	54.44
	Treptacantha usneoides	***Sphaerococcus coronopifolius***		
Deposit-feeders	0.3	0.366	0.0774	8.59
Solitary	0.472	0.505	0.0750	16.93
Gregarious	0.385	0.296	0.0750	25.25
Crawler	0.323	0.452	0.0631	32.26
Very Small (<2cm)	0.358	0.437	0.0566	38.54
Interstitial	0.67	0.774	0.0518	44.3
Small (2-5cm)	0.488	0.393	0.0514	50.01
	Halopteris scoparia	***Sphaerococcus coronopifolius***		
Interstitial	0.495	0.774	0.1080	9.74
None	0.549	0.804	0.1000	18.8
Gregarious	0.402	0.296	0.0884	26.8
Deposit-feeders	0.198	0.366	0.0749	33.57
Temporary	0.322	0.136	0.0727	40.15
Small (2-5cm)	0.445	0.393	0.0670	46.21
Very Small (<2cm)	0.387	0.437	0.0661	52.19
	Treptacantha usneoides	***Saccorhiza polyschides***		
Crawler	0.323	0.522	0.0884	9.75
Deposit-feeders	0.3	0.179	0.0755	18.08
Gregarious	0.385	0.509	0.0659	25.36
Omnivores	0.36	0.205	0.0624	32.25
Solitary	0.472	0.476	0.0589	38.75
Interstitial	0.67	0.611	0.0589	45.24
Deposit-feeders/Grazer	0.255	0.376	0.0541	51.22

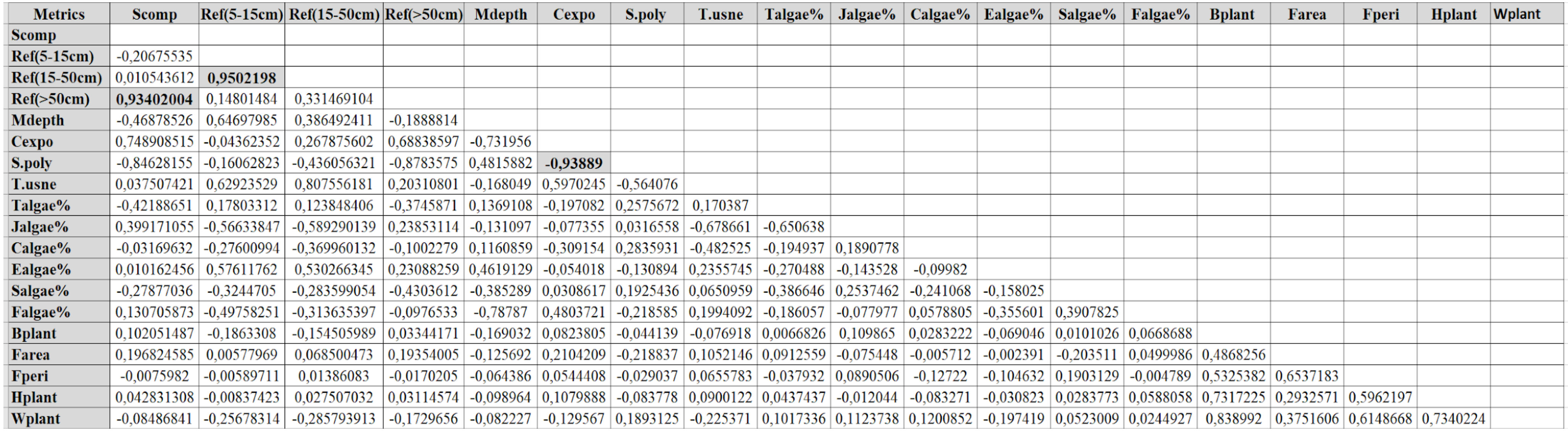
Table A7 (continued)

Trait categories	*Average value*	*Average value*	*Average squared distance*	*Cumulative contribution of the trait categories (%)*
	Halopteris scoparia	***Saccorhiza polyschides***		
Deposit-feeders/Grazer	0.146	0.376	0.0844	8.83
Crawler	0.358	0.522	0.0766	16.84
Gregarious	0.402	0.509	0.0721	24.39
Small (2-5cm)	0.445	0.504	0.0626	30.94
None	0.549	0.724	0.0608	37.29
Predator	0.251	0.0991	0.0605	43.63
Interstitial	0.495	0.611	0.0579	49.68
Solitary	0.476	0.476	0.0441	54.29
	Sphaerococcus coronopifolius	***Saccorhiza polyschides***		
Gregarious	0.296	0.509	0.1110	11.73
Deposit-feeders	0.366	0.179	0.0995	22.21
Crawler	0.452	0.522	0.0748	30.09
Interstitial	0.774	0.611	0.0727	37.75
Solitary	0.505	0.476	0.0680	44.91
Deposit-feeders/Grazer	0.217	0.376	0.0570	50.92

Appendix B

Metrics	XS	M	ML	S	SM	XL	Omn	Herb	Macro	Micro	Detri	Detri/Herb	Detri/Micro	Herb/Detri/Omn/Micro	Herb/Omn	Sus-feed	Carr-feed	Sus/Dep-feed	Dep-feed	Graz	Parr	Pred	Dep-feed/Graz	Dom	Dfo	Din	Epi	Fos	Ifo	Int	Sess	Swim	Craw	Burr	Burr/Craw	Swim/Craw	Burr/Swim	Swim/Craw/Burr	None	Temp	Perm	Soli	Greg	Soli/Greg	Soli/Col
XS																																													
M	-0,22121																																												
ML	-0,18927	-0,06309																																											
S	-0,68664	-0,05755	-0,22641																																										
SM	-0,37875	0,226031	-0,0742	-0,09572																																									
XL	0,013513	-0,04583	-0,02251	0,042977	-0,01478																																								
Omn	-0,13414	0,202855	-0,18898	0,27207	-0,07079	-0,01834																																							
Herb	-0,05574	0,336871	-0,10682	0,009199	0,19575	-0,14889	-0,06744																																						
Macro	-0,18734	0,139482	-0,00584	0,028235	0,380317	-0,00801	-0,17698	0,099466																																					
Micro	0,029951	-0,25405	-0,14317	0,158776	-0,20706	-0,11857	-0,02426	-0,26612	-0,02732																																				
Detri	0,309211	-0,05706	-0,04464	-0,37418	0,320785	0,064937	-0,28096	-0,05076	-0,1128	-0,26262																																			
Detri/Herb	0,042537	-0,27614	-0,05357	0,173648	-0,2023	0,083423	-0,42822	-0,03344	0,040248	-0,29909	-0,2711																																		
Detri/Micro	-0,03659	-0,0618	-0,01586	0,090386	-0,00332	0,420317	0,103279	-0,0495	-0,02313	-0,07052	-0,0329	0,0231734																																	
Herb/Detri/Omn/Micro	-0,30578	0,015572	0,821154	-0,0588	-0,0008	0,078945	-0,24895	-0,12725	0,024747	-0,07303	-0,0806	-0,117809	0,01172																																
Herb/Omn	-0,14756	-0,04583	-0,05323	0,221416	-0,02766	-0,02273	-0,28989	0,045715	0,031005	-0,1473	-0,0543	0,4899284	-0,03065	-0,07762142																															
Sus-feed	-0,18074	0,1376	-0,06314	-0,17207	0,818612	-0,08393	-0,06637	0,207881	0,118087	-0,24902	0,471	-0,218911	0,027789	-0,01737079	0,034959																														
Carr-feed	-0,39786	0,200389	-0,0545	0,263885	0,36339	0,200442	-0,12607	0,089057	0,515079	-0,08725	-0,0685	-0,033056	0,151161	0,28149403	-0,13813	0,170494																													
Sus/Dep-feed	0,210023	0,000314	-0,01233	-0,22874	-0,05529	0,26201	0,354761	-0,33381	-0,27725	-0,02349	-0,2275	0,0353636	0,145268	-0,02509812	-0,15512	-0,1006	-0,13354																												
Dep-feed	0,308847	0,005952	0,270102	-0,24289	-0,28892	-0,09375	0,063617	-0,04394	-0,22577	0,035724	0,394	-0,38724	-0,16719	0,12663092	-0,1588	-0,189	-0,39976	-0,34588																											
Graz	-0,22601	-0,20224	0,001503	0,251249	0,067548	-0,08871	-0,06688	0,236729	0,328967	-0,0998	-0,1366	0,2200994	0,056887	-0,13694354	0,159207	-0,07249	0,145761	-0,35593	-0,00963																										
Parr	-0,06621	-0,10071	0,043499	-0,04197	0,19342	0,003461	-0,22098	0,025262	0,431468	0,251032	-0,0444	-0,059138	-0,03821	0,04646138	0,00041	0,172805	0,138511	-0,02099	-0,30751	-0,05397																									
Pred	-0,34583	-0,1004	-0,11981	0,470422	-0,01169	-0,09008	0,267778	-0,22726	-0,00557	0,523235	-0,1525	-0,338246	0,093092	0,02946439	-0,12546	-0,02643	0,144004	-0,04543	-0,33267	-0,20944	0,150749																								
Dep-feed/Graz	0,067207	-0,08825	-0,11771	0,12732	-0,11859	0,038472	-0,38913	0,335689	0,08656	-0,41559	-0,2675	**0,9099904**	-0,03106	-0,16690344	0,457314	-0,142	-0,00742	-0,0721	-0,34731	0,196416	-0,09395	-0,42929																							
Dom	-0,11143	0,111355	-0,05646	-0,11792	0,532832	0,320805	0,154785	0,11035	-0,22305	-0,17246	0,32897	-0,307953	0,172137	0,07038881	-0,13567	0,62963	0,035146	0,242005	-0,15037	-0,22867	-0,05196	0,077003	-0,2221309																						
Dfo	0,076975	-0,17285	0,156252	-0,06403	-0,13767	0,229784	-0,0921	-0,37621	-0,04004	-0,0039	-0,1218	0,3224935	0,042007	0,07460217	0,113749	-0,13309	-0,05057	0,257018	-0,25812	-0,11755	0,076454	0,088797	0,161239	-0,07783																					
Din	0,407696	-0,09805	-0,04759	-0,3329	-0,17071	-0,00094	0,146813	-0,28323	-0,21335	0,064499	-0,1565	0,0622636	-0,08689	-0,01196096	-0,09807	-0,08475	-0,09317	0,742108	-0,27795	-0,21524	0,068319	-0,06948	-0,0476692	0,024435	0,302354																				
Epi	-0,27954	-0,04973	-0,07041	0,382523	0,053151	-0,03681	0,367977	-0,03103	-0,02781	0,100101	0,01341	-0,318956	0,11221	0,03496629	-0,10615	0,191862	0,144765	-0,12857	-0,27926	-0,15473	0,203638	0,799152	-0,3400953	0,232917	0,086276	-0,10161																			
Fos	-0,03717	-0,18503	0,182255	0,158938	-0,13009	-0,00962	-0,10801	-0,01351	0,137338	-0,05045	-0,1889	0,390667	0,397001	0,02451349	0,076565	-0,08189	0,067161	0,026029	-0,24359	0,179101	0,105577	0,063305	0,28724865	-0,28736	0,140763	-0,03061	0,028885																		
Ifo	-0,21738	0,078899	**0,909043**	-0,15312	-0,1441	-0,0448	-0,00661	-0,14448	0,066333	-0,1709	-0,1475	-0,111102	0,006402	0,75257452	-0,0731	-0,15327	-0,06453	0,048826	0,282525	0,01857	-0,01063	-0,11552	-0,1601141	-0,10659	0,118999	-0,04925	-0,07402	0,147981																	
Int	0,064077	-0,05752	-0,35741	0,220692	-0,00672	-0,10284	-0,26409	0,27933	0,213795	0,068619	0,10965	0,2554763	-0,10777	-0,36070243	0,189102	-0,14235	0,042829	-0,49881	0,31482	0,324646	-0,12621	-0,33349	0,35272318	-0,39372	-0,43951	-0,49607	-0,46952	0,003608	-0,39541																
Sess	-0,11622	0,249395	-0,08651	-0,20939	0,721212	-0,07187	0,025982	0,28848	-0,02343	-0,20446	0,53234	-0,425181	-0,09638	-0,00950459	-0,08346	0,854485	0,076984	-0,1051	-0,02547	-0,11183	0,03002	0,029919	-0,2768819	0,756239	-0,20966	-0,04287	0,22186	-0,30831	-0,13631	-0,22198															
Swim	-0,11749	0,219368	-0,14959	0,20935	-0,04956	-0,12959	0,493598	0,237863	0,182473	0,103895	-0,1747	-0,398256	-0,2011	-0,19020341	-0,15569	-0,16793	-0,04357	-0,25811	0,514235	0,252344	-0,08355	-0,16279	-0,2602643	-0,1781	-0,41715	-0,28974	-0,14659	-0,18416	-0,02024	0,408912	-0,04858														
Craw	0,056845	-0,31134	-0,17898	0,162652	-0,07713	-0,06256	-0,64109	-0,14269	0,167451	-0,00605	0,17124	0,6670428	-0,01283	-0,20197451	0,385086	-0,142	0,052936	-0,26627	-0,20578	0,197983	0,103199	-0,07416	0,53939743	-0,39217	0,047515	-0,14444	-0,24965	0,242005	-0,26548	0,503238	-0,29747	-0,43735													
Burr	0,008083	-0,17253	0,262634	-0,10997	0,061452	0,148605	-0,03271	-0,27474	0,032943	-0,03201	-0,0144	0,204426	0,042751	0,0429093	0,062484	0,062049	-0,04709	0,263145	-0,23169	-0,0782	0,28953	0,035963	0,07107364	-0,00777	0,781955	0,17466	0,091085	0,344118	0,174236	-0,37266	-0,12939	-0,31438	-0,03931												
Burr/Craw	-0,05215	0,368512	-0,03768	-0,06826	0,255316	0,260353	0,256527	0,51558	0,10986	-0,29165	-0,1174	-0,106908	0,225027	-0,06767808	-0,14085	0,18101	0,023767	0,267102	-0,19039	-0,25351	0,121542	-0,1176	0,16004817	0,39616	-0,13163	-0,1792	0,00371	0,055412	0,035262	-0,0557	0,161108	0,092009	-0,35205	0,091735											
Swim/Craw	0,07135	-0,10121	-0,11396	0,107625	-0,14369	0,014939	0,494239	-0,292	-0,3409	0,035516	-0,0719	-0,179354	0,164541	-0,01794061	-0,13602	0,048848	-0,02025	0,437143	-0,2937	-0,22377	-0,18647	0,529852	-0,2958614	0,205518	0,256738	0,546674	0,634684	-0,02878	-0,09756	-0,6323	0,099161	-0,29973	-0,30859	0,082399	-0,20243										
Burr/Swim	0,38818	-0,21971	-0,09934	-0,07607	-0,41599	-0,05347	0,051536	0,011775	-0,25359	0,483212	-0,1255	-0,102044	-0,10552	-0,17605734	-0,10155	-0,31091	-0,34057	-0,17223	0,547191	0,124052	-0,21636	-0,17919	-0,1033819	-0,21677	-0,20672	-0,05078	-0,2224	-0,07396	-0,14121	0,353983	-0,23917	0,410239	-0,17387	-0,23474	-0,24242	-0,14338									
Swim/Craw/Burr	-0,315	-0,00385	0,810255	-0,03873	-0,00102	0,0693	-0,21818	-0,13036	0,079535	-0,08835	-0,0667	-0,135607	0,038343	**0,96683707**	-0,08723	-0,04326	0,302556	-0,08039	0,177738	0,005801	0,002205	-0,00306	-0,1868827	0,041783	0,038638	-0,05852	0,000145	0,00986	0,794385	-0,31638	-0,02244	-0,11235	-0,20383	-0,00229	-0,10511	-0,05845	-0,15832								
None	-0,09677	-0,04177	0,039442	0,243232	-0,09202	-0,13046	-0,30595	0,230889	0,235014	0,025319	-0,0107	0,2499131	-0,06562	0,0168108	0,173693	-0,25829	0,051545	-0,51335	0,434771	0,390966	-0,13553	-0,38317	0,31444645	-0,48066	-0,44815	-0,53334	-0,52762	0,10417	0,044003	0,883434	-0,3271	0,416013	0,441528	-0,39356	-0,08878	-0,70526	0,323653	0,084950614							
Temp	0,103641	-0,18126	0,065204	0,006647	-0,14025	0,217031	0,350651	-0,34363	-0,18382	0,043839	-0,1354	-0,034527	0,162469	0,06483815	-0,1155	0,008886	-0,01972	0,539722	-0,42958	-0,31517	0,156067	0,484657	-0,1673853	0,268213	0,597143	0,534447	0,607027	0,145362	0,045534	-0,78682	-0,01134	-0,43422	-0,29377	0,554433	0,056782	0,778702	-0,25827	-4,3818E-05	-0,84311						
Perm	-0,11622	0,249395	-0,08651	-0,20939	0,721212	-0,07187	0,025982	0,28848	-0,02343	-0,20446	0,53234	-0,425181	-0,09638	-0,00950459	-0,08346	0,854485	0,076984	-0,1051	-0,02547	-0,11183	0,03002	0,029919	-0,2768819	0,756239	-0,20966	-0,04287	0,22186	-0,30831	-0,13631	-0,22198	**1**	-0,04858	-0,29747	-0,12939	0,161108	0,099161	-0,23917	-0,02243662	-0,3271	-0,01134					
Soli	0,106909	-0,12489	0,167104	0,074596	-0,48115	0,027297	0,148373	-0,08937	-0,15254	0,07175	-0,4777	0,2357071	-0,126	0,14070234	0,060025	-0,49516	-0,13948	0,222296	0,257759	0,134102	-0,23936	-0,39567	0,20135529	-0,25415	-0,08798	0,236543	-0,43931	-0,10353	0,206905	0,162446	-0,44712	0,367644	-0,12533	-0,24675	-0,14461	-0,11313	0,52054	0,171489641	0,311386	-0,16311	-0,44712				
Greg	-0,37188	0,040149	-0,06069	0,289813	0,43654	0,064433	0,064189	0,086738	0,280076	0,038546	-0,0848	0,0040313	0,228866	0,02622919	0,042011	0,377354	0,282276	-0,04204	-0,55058	0,028516	0,30325	0,526302	0,00872417	0,238569	0,337557	-0,09751	0,54194	0,325979	-0,06405	-0,29603	0,254376	-0,29361	-0,02984	0,450148	0,237814	0,266927	-0,49583	0,004650547	-0,34338	0,430468	0,254376	-0,7063			
Soli/Greg	-0,20915	-0,08318	0,131538	0,075052	0,086137	-0,02346	-0,0417	0,241133	-0,11644	-0,08154	0,09244	-0,023777	-0,06524	-0,06219696	-0,06049	0,123025	0,034515	-0,16209	-0,03771	0,357875	0,111497	-0,02813	-0,0323808	0,058201	-0,1789	-0,12648	0,127506	0,024677	-0,02485	0,001826	0,11361	0,030209	-0,02279	0,003725	-0,07024	-0,07883	0,110006	-0,01285654	-0,00519	-0,05643	0,11361	0,061674	-0,1432		
Soli/Col	0,014672	-0,10155	0,080346	-0,16856	0,20355	-0,01457	-0,2373	0,220016	-0,08598	-0,18517	0,37532	-0,054395	0,014733	-0,00925344	-0,01988	0,450338	-0,1099	-0,18733	-0,00506	-0,05515	-0,0257	-0,04857	0,02833362	0,299019	-0,17941	-0,11517	0,092664	-0,09251	-0,01607	-0,07061	0,4338	-0,27002	0,072041	-0,17034	0,044315	0,008705	-0,08611	-0,02744417	-0,11204	-0,06738	0,4338	-0,19902	-0,08532	0,270641	

Figure B1- Draftsmen plot with Pearson's correlations between the functional traits categories. Traits with correlations higher than |0,90| were assumed as proxies (shaded values). Trait code: Potential size category: XS- Very small (<2cm), M- Medium (10-15cm), ML- Medium-large (15-30cm), S- Small (2-5cm), SM- Small-medium (5-10cm), XL- Very Large (>50cm); Diet category: Omn- Omnivores, Herb- Herbivores, Macro- Macrocarnivores, Micro- Microcarnivores, Detri- Detritivores, Detri/Herb- Detritivores/Herbivores, Detri/Micro- Detritivores/Microcarnivores, Herb/Detri/Omn/Micro- Herbivores/Detritivores/Omnivores/Microcarnivores, Herb/Omn- Herbivores/Omnivores; Feeding mode category: Sus-feed- Suspension-feeders, Carr-feed- Carrion-feeders, Sus/Dep-feed- Suspension/Deposit-feeders, Dep-feed- Deposit-feeders, Graz- Grazer, Par- Parasite, Pred- Predator, Dep-feed/Graz- Deposit-feeders/Gazer; Adult life habit category: Dom- Domicolous, Dfo- Domicolous/Fossorial, Din- Domicolous/Interstitial, Epi- Epi-/endozoic or epi-/endophytic, Fos- Fossorial, Ifo- Interstitial/Fossorial, Int- Interstitial; Adult movement category: Sess- Sessile, Swim- Swimmer, Craw- Crawler, Burr- Burrower, Burr/Craw- Burrower/Crawler, Swim/Craw- Swimmer/Crawler, Burr/Swim- Burrower/Swimmer, Swim/Craw/Burr- Swimmer/Crawler/Burrower; Degree of attachment category: None, Temp- Temporary, Perm- Permanent; Sociability category: Soli- Solitary, Greg- Gregarious, Soli/Greg- Solitary/Gregarious, Soli/Col- Solitary/Colonial.



Metrics	Scomp	Ref(5-15cm)	Ref(15-50cm)	Ref(>50cm)	Mdepth	Cexpo	S.poly	T.usne	Talgae%	Jalgae%	Calgae%	Ealgae%	Salgae%	Falgae%	Bplant	Farea	Fperi	Hplant	Wplant
Scomp																			
Ref(5-15cm)	-0,20675535																		
Ref(15-50cm)	0,010543612	**0,9502198**																	
Ref(>50cm)	**0,93402004**	0,14801484	0,331469104																
Mdepth	-0,46878526	0,64697985	0,386492411	-0,1888814															
Cexpo	0,748908515	-0,04362352	0,267875602	0,68838597	-0,731956														
S.poly	-0,84628155	-0,16062823	-0,436056321	-0,8783575	0,4815882	**-0,93889**													
T.usne	0,037507421	0,62923529	0,807556181	0,20310801	-0,168049	0,5970245	-0,564076												
Talgae%	-0,42188651	0,17803312	0,123848406	-0,3745871	0,1369108	-0,197082	0,2575672	0,170387											
Jalgae%	0,399171055	-0,56633847	-0,589290139	0,23853114	-0,131097	-0,077355	0,0316558	-0,678661	-0,650638										
Calgae%	-0,03169632	-0,27600994	-0,369960132	-0,1002279	0,1160859	-0,309154	0,2835931	-0,482525	-0,194937	0,1890778									
Ealgae%	0,010162456	0,57611762	0,530266345	0,23088259	0,4619129	-0,054018	-0,130894	0,2355745	-0,270488	-0,143528	-0,09982								
Salgae%	-0,27877036	-0,3244705	-0,283599054	-0,4303612	-0,385289	0,0308617	0,1925436	0,0650959	-0,386646	0,2537462	-0,241068	-0,158025							
Falgae%	0,130705873	-0,49758251	-0,313635397	-0,0976533	-0,78787	0,4803721	-0,218585	0,1994092	-0,186057	-0,077977	0,0578805	-0,355601	0,3907825						
Bplant	0,102051487	-0,1863308	-0,154505989	0,03344171	-0,169032	0,0823805	-0,044139	-0,076918	0,0066826	0,109865	0,0283222	-0,069046	0,0101026	0,0668688					
Farea	0,196824585	0,00577969	0,068500473	0,19354005	-0,125692	0,2104209	-0,218837	0,1052146	0,0912559	-0,075448	-0,005712	-0,002391	-0,203511	0,0499986	0,4868256				
Fperi	-0,0075982	-0,00589711	0,01386083	-0,0170205	-0,064386	0,0544408	-0,029037	0,0655783	-0,037932	0,0890506	-0,12722	-0,104632	0,1903129	-0,004789	0,5325382	0,6537183			
Hplant	0,042831308	-0,00837423	0,027507032	0,03114574	-0,098964	0,1079888	-0,083778	0,0900122	0,0437437	-0,012044	-0,083271	-0,030823	0,0283773	0,0588058	0,7317225	0,2932571	0,5962197		
Wplant	-0,08486841	-0,25678314	-0,285793913	-0,1729656	-0,082227	-0,129567	0,1893125	-0,225371	0,1017336	0,1123738	0,1200852	-0,197419	0,0523009	0,0244927	0,838992	0,3751606	0,6148668	0,7340224	

Figure B2- Draftsmen plot with Pearson’s correlations between macroalgal and environmental variables. Variables with correlations higher than |0,90| were assumed as proxies (shaded values). Code for variables: Scomp- Structural complexity; Ref(5-15cm)- Number refuges with sizes between 5-15cm; Ref(15-50cm)- Number refuges with sizes between 15-50cm; Ref(>50cm)- Number refuges with sizes larger than 50cm; Mdepth- Mean depth (m); Cexpo- Coast exposure; S.poly- Density of *S.polyschides* (N/m^2); T.usne- Density of *T.usneoides* (N/m^2); Talgae%- Thick-Leathery Algal cover (%); Jalgae%- Jointed-Calcareous Algal cover (%); Calgae%- Coarsely-Branched Algal cover (%); Ealgae%- Encrusting Algal cover (%); Salgae%-Sheet Algal cover (%); Falgae%- Filamentous Algal cover (%); Bplant- Biomass per plant (dry weight in g); Farea- Fractal area (cm^2); Fperi- Fractal perimeter (cm); Hplant- Height per plant (cm); Wplant- Width per plant (cm).

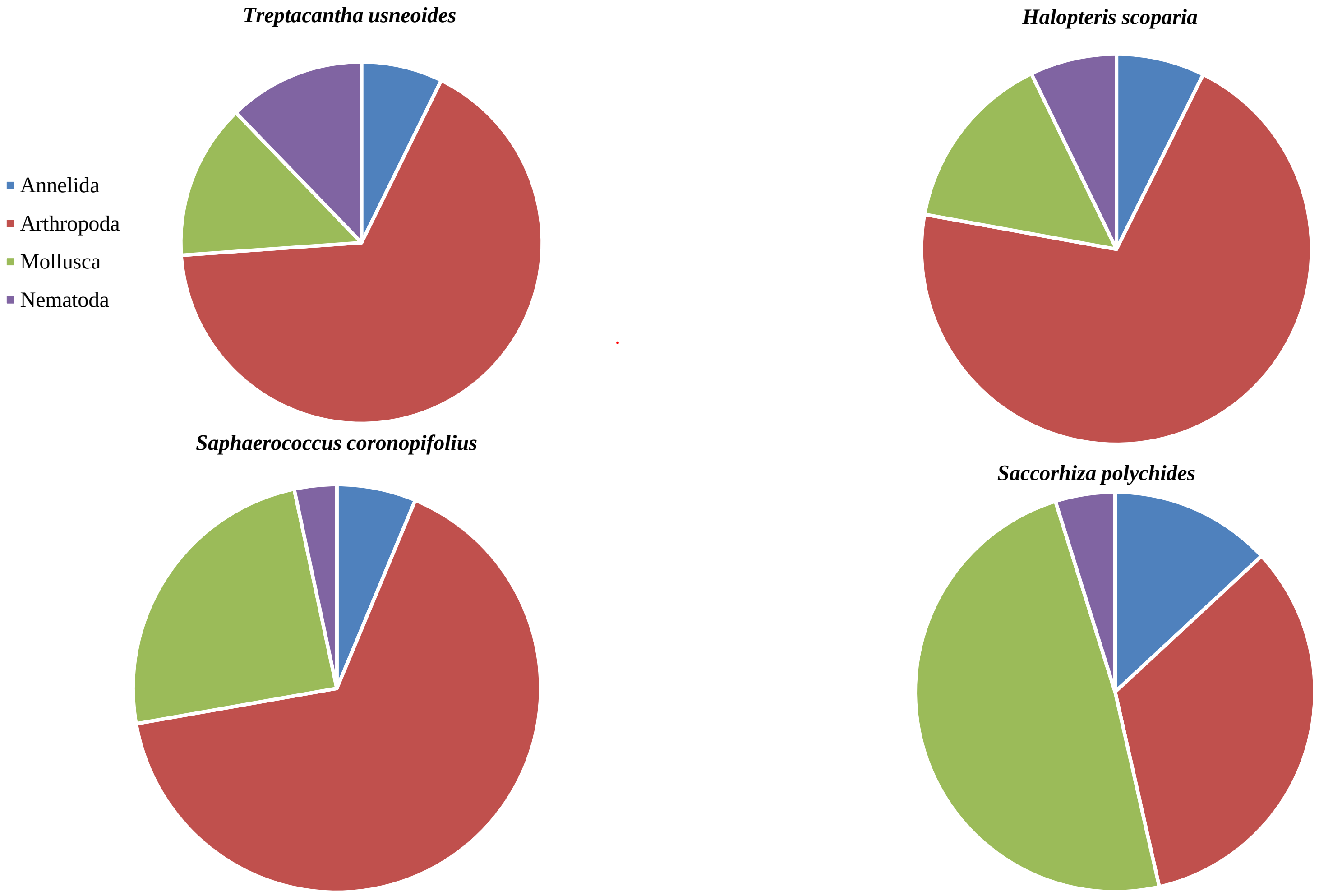
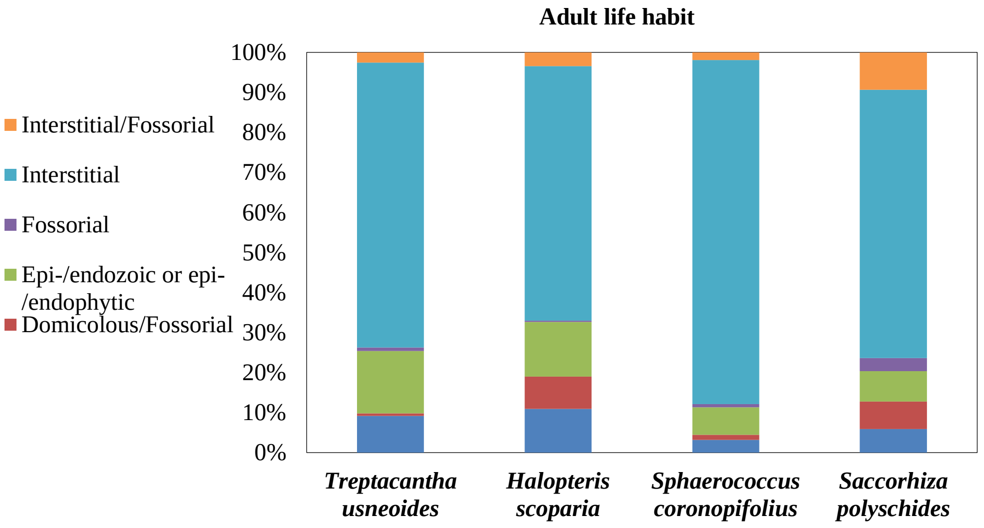
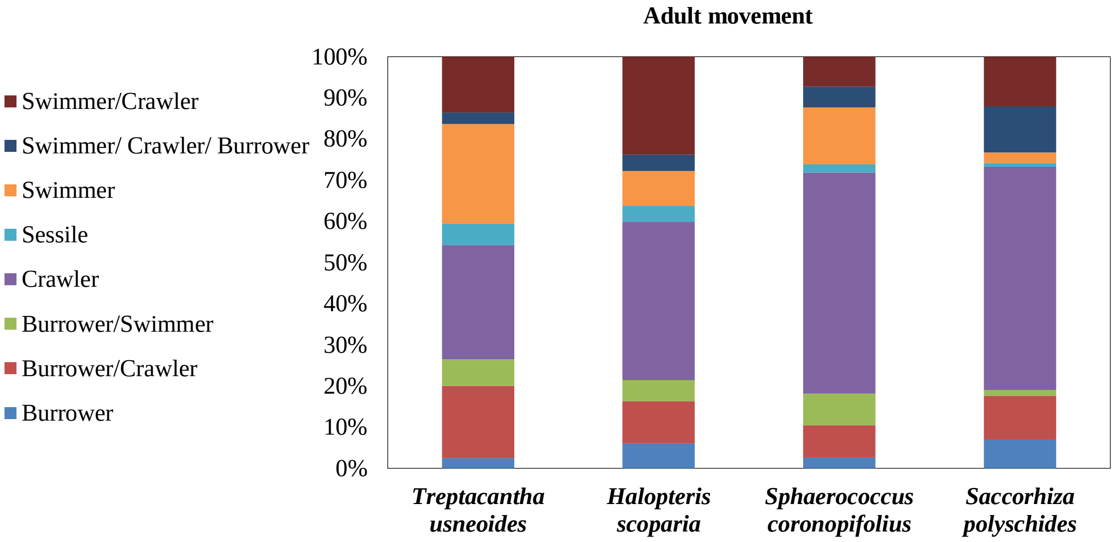
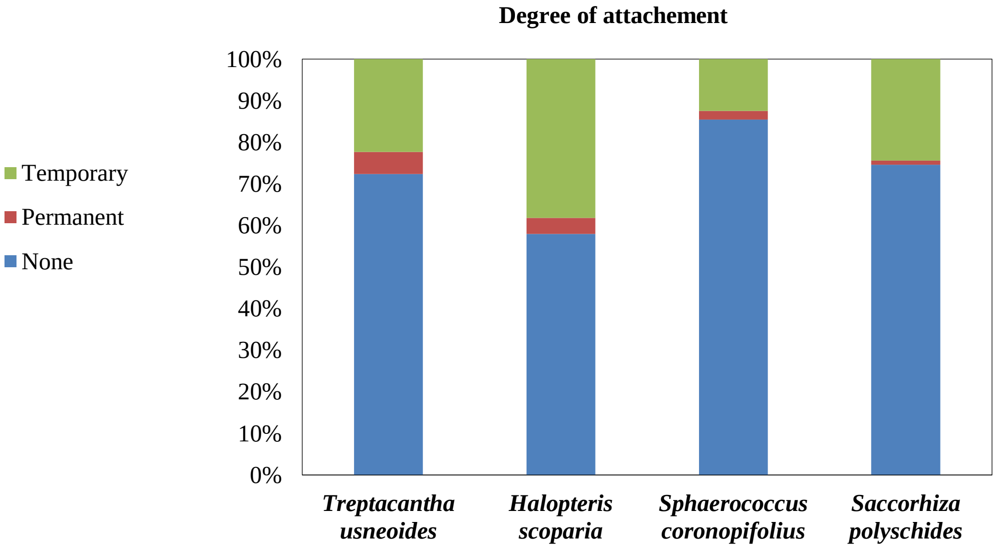
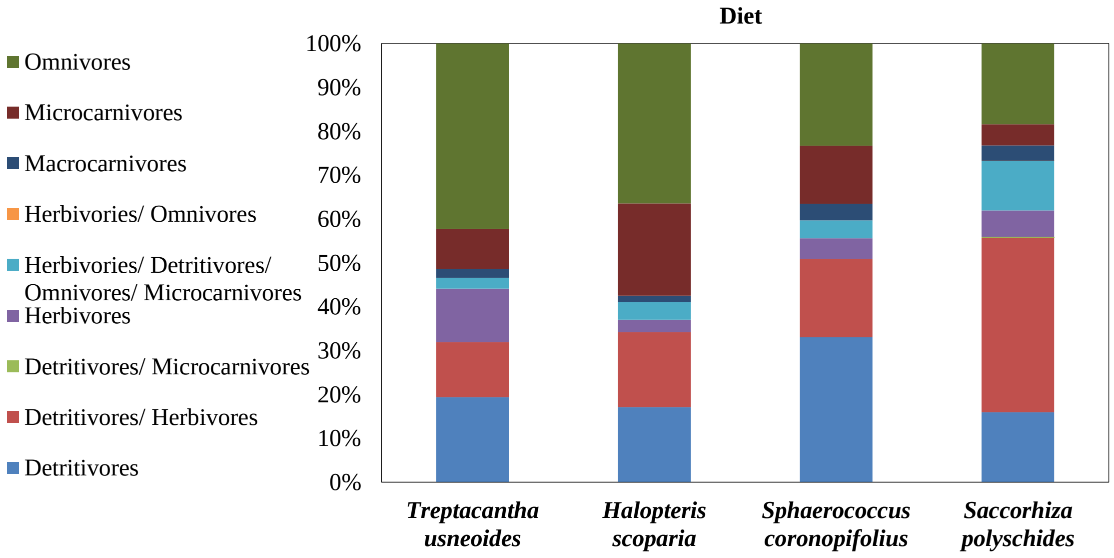


Figure B3- Dominance in terms of number of individuals of each phylum per HFS. Data expressed as percentage of individuals of each phylum in relation to the total number collected in each HFS. Chordata, Echinodermata, Nemertea, and Platyhelminthes are not included since they comprised less than 0.5% of total abundance.


Adult life habit


Adult movement


Degree of attachement


Diet

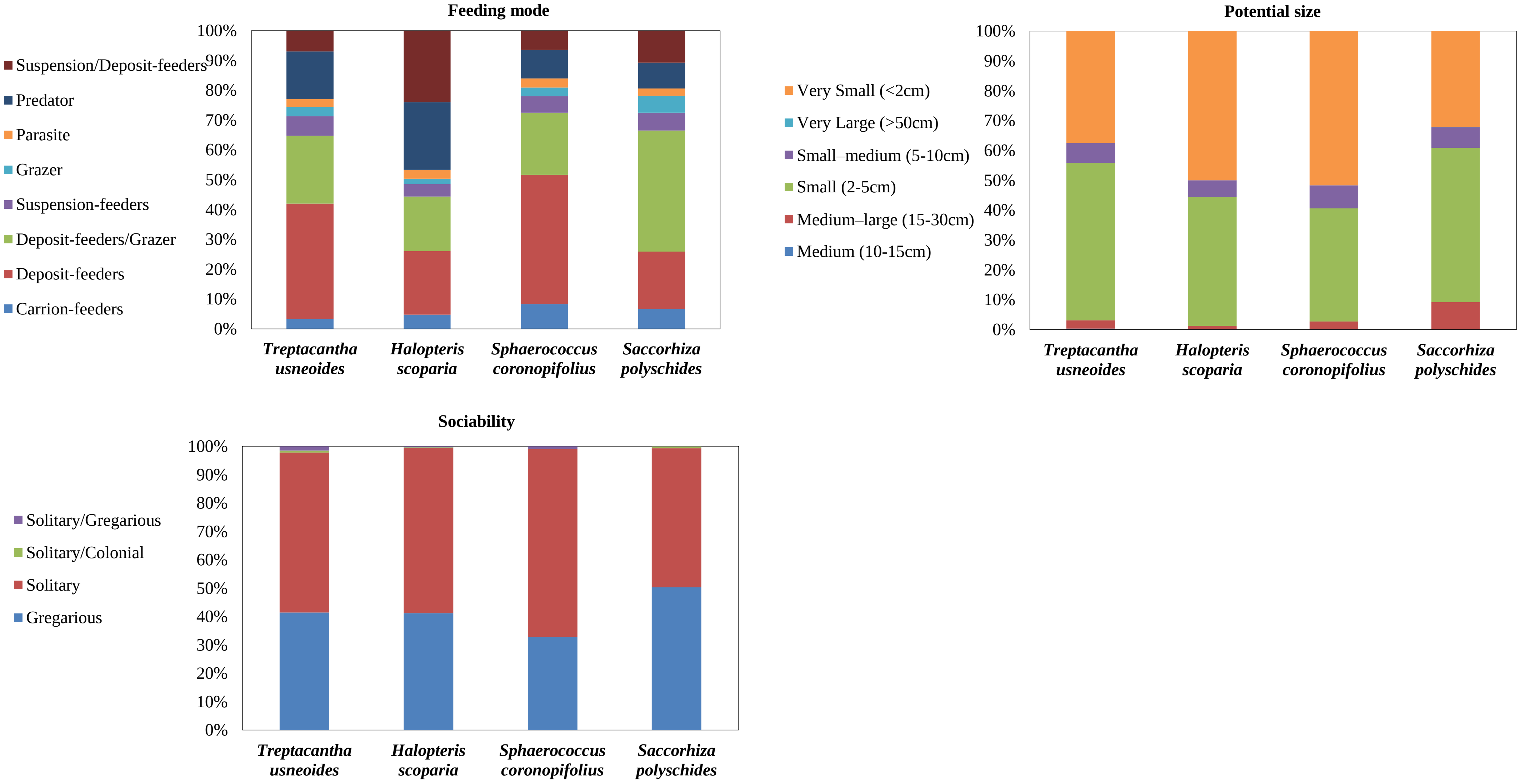


Figure B4- Proportion of different functional traits categories (%) per HFS host. Data are expressed as percentage of individuals belonging to each functional category in relation to the total number of epifauna collected in each HFS.